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THE GENERA OF SPHENOCLEACEAE AND
CAMPANULACEAE IN THE
SOUTHEASTERN UNITED STATES¹

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SPHENOCLEACEAE A. P. de Candolle, Prodr. 7(2): 548. 1839, nom. cons.

(SPHENOCLEA FAMILY)

A monogeneric family of one or two species of annual herbs that inhabit wet places. The plants are distinguished by nonmilky sap; erect, spongy, fistulous,

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Figure 1 (*Triodanis*) was prepared by Rachel A. Wheeler under the supervision of George K. Brizicky, from preserved material collected by Carroll Wood and Alan Strahler near Fort Meade, Florida (CEW 9020). Figure 2 (*Lobelia*) was drawn by Virginia Savage with the guidance of Carroll Wood (who also prepared the dissections), from plants cultivated by Alice F. Tryon in Lexington, Massachusetts (a, b, k, l, m) and from preserved flowers of plants grown by the late Richard J. Eaton in Lincoln, Massachusetts (c–j).

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somewhat succulent stems; simple, alternate, exstipulate, petiolate, entire leaves; terminal, densely spicate (the axes completely hidden), clearly acropetal, pedunculate inflorescences; perfect, actinomorphic, sessile flowers, each subtended by a bract and two bracteoles; green calyces with deltoid to suborbicular, imbricate lobes that encase both flower buds and fruits (and thereby render most of the inflorescence/infructescence green); white to pale yellow, caducous corollas with imbricate lobes; short filaments and rounded anthers; mostly inferior, bilocular ovaries with numerous ovules and large, spongy, axile placentae; and membranaceous, circumscissile, bilocular, many-seeded capsules. TYPE GENUS: *Sphenoclea* Gaertner.

1. ***Sphenoclea*** Gaertner, *Fruct. Sem. Pl.* 1: 113. 1788, nom. cons.³

Erect, glabrous annuals (reportedly sometimes perennials) of moist to wet places. Stems without milky sap, freely branched, somewhat succulent, hollow. Leaves ovate to elliptic; base cuneate, sometimes slightly oblique; apex acute to rounded, sometimes mucronate; venation pinnate and somewhat arcuate. Inflorescences terminating the main stem or axillary branches, acropetal, densely spicate, pedunculate. Flowers perfect, laterally compressed, sessile, attached by a narrowly elliptic, longitudinally oriented base and each subtended by a single, spatulate, acute to acuminate, green-tipped bract and 2 slightly smaller, more nearly linear, green-tipped bracteoles. Calyx synsepalous below, actinomorphic; lobes 5, deltoid to suborbicular, slightly erose, curved inward, imbricate, persistent and enlarging in fruit. Corolla sympetalous below, actinomorphic; lobes 5, alternate with the calyx lobes, rounded, slightly erose, curved inward, imbricate, exceeding the calyx at anthesis, caducous. Stamens 5, not connate, adnate to the corolla and alternate with its lobes; filament short; anther rounded, 2-locular at anthesis, longitudinally dehiscent. Ovary mostly inferior, 2-locular; placentae spongy, stipitate, axile; style short or not apparent, collecting hairs absent; stigma capitate, slightly bilobed, sessile or nearly so. Ovules numerous, anatropous, unitegmic, tenuinucellate. Fruit a cuneate-obconical, 2-locular, membranaceous, circumscissile capsule, mostly encased in the persistent calyx lobes. Seeds numerous, small, oblong, yellowish brown, lustrous, longitudinally striate with indistinct pits between the ridges; endosperm cellular; embryo straight, filling the seed, its development of the *Onagrad* type. (*Pongati* Adanson, nom. illeg.; *Pongatium* Juss., nom. illeg.) TYPE SPECIES: *S. zeylanica* Gaertner. (Name probably from Greek *sphēn*, a wedge, most likely in reference to the capsule, which is wedge shaped below by compression; Gaertner's original description of *Sphenoclea* included the phrase "capsula infera, cuneiformi-compressa, bilocularis, circumscissa.")

A small genus composed of one or two species of herbs. *Sphenoclea zeylanica* Gaertner, $2n = 24$, and the West African endemic *S. Pongatium* DC. have been recognized, but the latter is commonly lumped under *S. zeylanica*, and almost all of the literature deals with plants to which this name has been applied.

³Conservation superfluous; see Rickett & Stafleu, *Taxon* 9: 122. 1960. *Pongatai* Adanson (1757) is not validly published, and *Pongatium* Juss. (1789) is a later synonym.

Sphenoclea differs most conspicuously from members of the Campanulaceae in its densely spicate inflorescences. In habit the genus is often said to resemble *Phytolacca* (Phytolaccaceae). Because of this vegetative similarity and several unspecified anatomical features, Airy Shaw suggested that *Sphenoclea* is taxonomically allied with *Phytolacca* and unrelated to the Campanulaceae. However, although Kovanda proposed a connection between *Sphenoclea* and the Lythraceae, such a position is at odds with the overwhelming majority of botanical opinion.

On the bases of anatomy and morphology of flowers, fruits, seeds, and seedlings, Monod considered the Sphenocleaceae and the Campanulaceae to be related, although Gupta concluded that differences in floral vasculature between *Sphenoclea*, *Campanula*, and *Lobelia* were not important enough to warrant a separate family for *Sphenoclea*. Maheshwari summarized both anatomical and embryological evidence, including that provided by Subramanyam (1950), and concluded that *Sphenoclea* is related neither to the Phytolaccaceae nor to the Primulaceae (a relationship that Airy Shaw had also considered). In contrast to the Phytolaccaceae, both *Sphenoclea* and members of the Campanulaceae lack anomalous secondary growth and have anatropous, unitegmic, tenuinucellate (vs. anacampylotropous, bitegmic, crassinucellate) ovules and cellular (vs. free-nuclear) endosperm with well-developed haustoria (vs. no haustoria). Hutchinson (1973) and Corner also pointed out some essential differences between *Sphenoclea* and *Phytolacca*, and Cronquist noted that *Sphenoclea* is embryologically and palynologically similar to the Campanulaceae.

Although most botanists have favored an alliance with the Campanulaceae, opinions have varied regarding the taxonomic level at which *Sphenoclea* should be recognized. De Candolle and Boissier each placed the Sphenocleaceae near the Campanulaceae, and both Wagenitz and Cronquist recognized it as one of a number of families in the Campanulales. Corner, Dunbar (1975b), Monod, and Subramanyam (1950), among others, have recognized the genus as a monotypic family related to the Campanulaceae. Baillon's treatment of the Campanulaceae included tribes Sphenocleae, Campanuleae, and Lobelieae, and Schönland recognized subfamilies Campanuloideae (including tribe Sphenocleae), Cyphioideae, and Lobelioideae. Bentham & Hooker placed the Campanuleae (including *Sphenoclea*), Lobelieae, and Cyphieae in their Campanulaceae. Dahlgren, Fedorov, Takhtajan, Thorne (1976), and Wilbur are among the modern systematists who have included *Sphenoclea* in the Campanulaceae (see also Moeliono & Tuyn).

Chemical data regarding the affinities of *Sphenoclea* appear to be contradictory. According to Gibbs, raphides (used by Gibbs to mean crystals of calcium oxalate) are present in *Phytolacca* and some related genera but are probably absent from *Sphenoclea* and members of the Campanulaceae. Cronquist (1981), however, indicated the presence of calcium oxalate crystals in the Phytolaccaceae (said to be often raphides), as well as in *Sphenoclea* (whether they are raphides was not indicated).

Treatment of *Sphenoclea* as a separate family seems at this time to be largely a matter of opinion. The decision to do so here is at least in part intended to

accentuate differences that are especially apparent among plants of the southeastern United States. The Campanuloideae and Lobelioideae (and the intermediate and extraregional Cyphioideae) appear to be much more closely related to each other than to *Sphenoclea*. The only other family in the Southeast to have been allied with the Sphenocleaceae and the Campanulaceae is the Goodeniaceae. Although these three families were united by Cronquist at the ordinal level, most recent evidence suggests that the affinities of the Goodeniaceae lie elsewhere (see discussion under Campanulaceae). With the removal of the Goodeniaceae (and the related Brunoniaceae), recognition of the Sphenocleaceae within a more homogeneous and narrowly defined Campanulales seems even more justified.

In addition to having a densely spicate inflorescence, *Sphenoclea* differs from genera of the Campanulaceae in the absence of a specialized mechanism of pollen presentation, as well as in the lack of typical laticiferous phloem canals (although granules in some phloem cells may represent dried latex; see, however, Airy Shaw). Furthermore, *Sphenoclea* has circumscissile capsules, tetracytic instead of mostly anomocytic stomata (see Shah & Mathew), pericyclic stem sclerenchyma, and cluster crystals, instead of fine, mostly acicular ones (Metcalf & Chalk, 1950).

Sphenoclea zeylanica, $2n = 24$, sheds trinucleate pollen (Kausik & Subramanyam) that is subprolate, tricolporate, and reticulate (Cronquist). Dunbar (1975b) stated that the exine sculpturing (smooth but with round protrusions of varying size) has no relationship with the condition seen in the Campanulaceae.

Reportedly rare in South Carolina (Radford *et al.*) and evidently absent from tropical Florida (see Long & Lakela), *Sphenoclea zeylanica* occurs in moist soil or shallow water throughout most of the remainder of the Coastal Plain in the southeastern United States; it has also been reported from Texas (Correll & Johnston). The species is a native of the Old World tropics and is now widely established in warm areas of the Western Hemisphere. It was collected in Louisiana as early as 1898. Although almost exclusively indicated to be an annual, Radford and colleagues reported it as a perennial.

Sphenoclea zeylanica commonly grows as a weed in rice fields throughout the world. An exudate from the roots of living plants has been shown to serve as an effective and expedient control of the rice-root nematode, *Hirschmanniella oryzae* (Mohandas *et al.*). The pleasant-tasting leaves are eaten with rice by the Javanese (Uphof).

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CAMPANULACEAE A. L. de Jussieu, Gen. Pl. 163. 1789, nom. cons.

(BELLFLOWER FAMILY)

Erect, ascending, decumbent, sometimes prostrate [or caespitose], terrestrial to aquatic, laticiferous, annual, biennial, or perennial herbs (sometimes woody toward the base) [or shrubs or trees to 10 m tall]. Stems simple to much branched, often more so near the base, sometimes rhizomatous [or stems succulent]. Leaves simple, alternate, sometimes opposite or whorled (in 3's), exstipulate, sessile to petiolate, the margins entire, ciliate, undulate, serrate, crenate, or dentate, sometimes lobed. Inflorescences racemose (including globose, involucrate umbels, spikes, or panicles) or cymose, the flowers rarely solitary; floral bracts inconspicuous or leaflike. Flowers perfect [rarely carpellate or staminate, the plants then dioecious], sometimes cleistogamous (and then often with rudimentary or missing parts), sometimes bracteolate, resupinate in the Lobelioideae, proterandrous. Hypanthium sometimes extending shortly above the ovary, sometimes ribbed. Calyx synsepalous, mostly actinomorphic, often with a reflexed appendage in the sinuses between lobes, persistent in fruit; lobes 5 (3, 4, or 6), imbricate or valvate, often linear, frequently longer than the tube, opposite the axis of the inflorescence in the Campanuloideae, alternate in the Lobelioideae (but made opposite by resupination). Corolla sympetalous; lobes 5, alternate with the lobes of the calyx, either actinomorphic and campanulate to rotate (Campanuloideae) or zygomorphic and 2-lipped (Lobelioideae), with the 3 upper petals forming a lower 3-lobed lip and the other 2 forming an upper lip (after resupination) that is 2-lobed and sometimes cleft between the lobes [sometimes to the base of the corolla] [or sometimes all 5 petals more equally connate and less zygomorphic]. Stamens equal in number

to and alternate with the corolla lobes; filaments free from the corolla (and inserted on a disclike nectary) or inserted at its base, free below (connate above in the Lobelioideae); anthers bilocular, with introrse, longitudinal dehiscence, coherent and becoming free after anthesis in the Campanuloideae but connate in the Lobelioideae, in both subfamilies forming a tube into which pollen is released. Pollen 2–12-aperturate; in the Campanuloideae usually porate (rarely colporate) [or colpate] and spinulose; in the Lobelioideae colpate [or colporate] and reticulate. Gynoecium 2–5-carpellate (usually 3 in the Campanuloideae and 2 in the Lobelioideae), carpels fused into an inferior (or sometimes half-inferior) [rarely superior] ovary commonly bearing an annular nectariferous disc and usually with as many locules as carpels or sometimes more by the intrusion of false septa (Campanuloideae) or fewer by the disappearance of septa (Lobelioideae). Style with apical hairs that remove pollen from the anther tube as the base of the style elongates; stigma lobes 2–5, spreading apart after exceeding the anther tube. Ovules numerous on axile (sometimes parietal) placentae, anatropous, tenuinucellar, and with a single, massive integument; megagametophyte of the Polygonum type. Fruit a loculicidal capsule dehiscent by pores or slits either apically (i.e., within the persistent calyx lobes) or laterally [rarely indehiscent or a berry]. Seeds numerous, small; endosperm cellular, oily [rarely starchy]; haustoria at micropylar and chalazal ends; embryo usually straight, not filling the seed, its development of the Solanad type. (Including Lobeliaceae R. Br. Trans. Linn. Soc. London 12: 133. 1817, nom. cons.) TYPE GENUS: *Lobelia* L.

The family is here considered to include the subfamilies Campanuloideae and Lobelioideae Schönl., as well as the intermediate and extraregional Cyphioideae Schönl. As such, it consists of perhaps as many as 70 genera and 2000 species. The Campanulaceae are of cosmopolitan distribution, although they are best represented in temperate and subtropical regions; tropical species are mostly confined to high elevations. These plants rarely (if ever) grow in pure stands or otherwise occur as dominant vegetational components. Nevertheless, they are often conspicuous because of either showy flowers or unusual habit.

The Campanulaceae are distinguished most readily by a combination of characters including milky sap; rotate, campanulate, or bilabiate corollas; a specialized mechanism of pollen presentation (a stylar brush carries pollen out of and above a variously configured anther tube); and mostly inferior (but sometimes half-inferior or superior) ovaries with axile (rarely parietal) placentae and numerous ovules per locule. Although the varied inflorescences of the Campanulaceae are for the most part very different from the pseudanthium of the Compositae (Asteraceae) (a family that, except for its basal placenta and single ovule per locule, conforms to the foregoing criteria), the globose, involucrate umbel of *Jasione* approaches this design.

The Campanulaceae were placed by Cronquist in his Campanulales with the Brunoniaceae, Donatiaceae, Goodeniaceae, Pentaphragmataceae, Sphenocleaceae, and Stylidiaceae; the Campanulales of Takhtajan and of Thorne were similar to Cronquist's in content, except that Thorne excluded the Stylidiaceae

(including *Donatia* J. R. & G. Forster). Two noncampanulaceous members of the order are represented in the Southeast. *Scaevola Plumieri* (L.) Vahl (Goodeniaceae) is native to southern Florida and other tropical and subtropical areas outside of the Southeast (see Brizicky), and *Sphenoclea zeylanica* Gaertner (Sphenocleaceae) is a species of the Old World tropics that is widely naturalized in warm regions of the Western Hemisphere, including most of the Coastal Plain of North America (see preceding treatment). Carolin (1978) summarized arguments for a saxifragalean origin of the Campanulales (Thorne placed his Stylidiaceae near the Saxifragaceae), while Cronquist favored consideration of the Solanales or their close relatives.

Several botanists have suggested a relationship between the Campanulaceae and the Goodeniaceae, primarily because of similarities in embryology and in the mechanism of pollen presentation. However, the embryological similarities are based on some rather widely distributed character states, and the families differ in certain other embryological features (Vijayaraghavan & Malik). The styler structures involved in pollen collection (a cup, or indusium, in the Goodeniaceae; hairs in the Campanulaceae) were thought by Carolin (1960) and Cronquist to be analogous. Furthermore, Carolin (1978) has argued that the inferior ovaries of the two groups are not homologous. In his opinion, in the Campanulaceae (where some genera have an extension of the floral tube above the ovary), epigyny resulted from the fusion of a preformed tube of sepals, petals, and stamens to the ovary, while in the Goodeniaceae (where there is no extension above the ovary and, in some genera, a progressive departure of sepals, petals, and stamens from the tube), epigyny resulted from the centrifugal adnation of these parts.

The Goodeniaceae also differ from the Campanulaceae in their more complex cambial anatomy; in the absence of a latex system; in the presence of sclerenchymatous idioblasts (in leaf mesophyll, sometimes in stem cortex as well) and glandular trichomes (Metcalf & Chalk, 1950; but some species of *Lobelia* have glandular trichomes on the calyx lobes); in their lack of nectaries (but see Carolin, 1959) and of haustoria in the endosperm (Vijayaraghavan & Malik); in the absence of cystoliths (Cronquist); in their pollen (see below); in their complete lack of ellagic acid and tannins (Cronquist); and in the presence of iridoids (Dahlgren *et al.*, Jensen *et al.*). Jensen and colleagues discovered secoiridoids in two genera of Goodeniaceae (including *Scaevola*) and therefore concluded that the group should be recognized as an order distinct from the Campanulales and more closely related to the Gentianales, Dipsacales, and/or Cornales. Vijayaraghavan & Malik also favored a unifamilial Goodeniales, primarily on embryological grounds, but considered it very close to the Campanulales.

Some authors have proposed an origin of the Goodeniaceae within the Lobelioideae. However, although both groups have zygomorphic corollas with slits, the slit in the sympetalous corolla is made adaxial by resupination in the Lobelioideae, while in the Goodeniaceae it is adaxial and there is no resupination. Furthermore, the two-locular ovary of these groups is characteristic of a number of diverse families, and it has been interpreted by Carolin (1960), primarily on the basis of vascularization, to have been derived from two carpels

in the Lobelioideae and from four (accompanied by the loss of two septa) in the Goodeniaceae.

Carolin (1978) concluded that while the Campanulaceae are the nearest relatives of the Goodeniaceae, the relationship is not a close one. He considered the two groups to have evolved (presumably from a common ancestor) in Gondwanaland, the Campanulaceae in the west and the Goodeniaceae in the east. Takhtajan considered the Goodeniaceae (including the Brunoniaceae as a subfamily) to be less related to the remainder of the Campanulales and recognized the suborder Goodeniineae within that order.

The Campanulaceae are among a number of families that have traditionally been suggested to be ancestral to the Compositae (reviewed by Philipson, 1953). Many early botanists favored such a relationship on the basis of floral morphology, particularly the specialized mechanisms of pollen presentation in the two groups. However, similar specializations occur in several putatively unrelated families within the Asteridae and are therefore thought not to be reliable indicators of relationships (Cronquist). Internal phloem, laticifers, and inulin occur in both the Campanulaceae and the Compositae but are sporadic in other families as well. In nodal anatomy the Compositae (and Goodeniaceae) are trilacunar (or rarely multilacunar), whereas the Campanulaceae are always unilacunar, a condition generally thought to represent an evolutionary reduction from more complex types.

In attempts to determine the origin of the Compositae, consideration of the inflorescence has pointed to both the Campanulaceae and the Dipsacaceae. Although the precise nature of the capitulum in the Compositae is not clear, it has often been compared to what is usually considered to be a cymose head in the Dipsacaceae. The plasticity of the inflorescence in the Campanulaceae is well known, and although both cymose and racemose (as well as intermediate) types occur in the family, the latter is more characteristic and is thought to represent the condition seen in *Jasione* (see Carolin, 1967), a genus of Campanulaceae with involucrate umbels. Nevertheless, although the pedicels of both the Compositae and *Jasione* lack bracteoles, such structures are present in the dipsacaceous inflorescence (Philipson, 1948). In addition, the involucre bracts of the Compositae lack meristematic tissue in their axils. Although the bracts of the Dipsacaceae subtend flowers, the bract axils of *Jasione* are often sterile by floral abortion. Philipson (1948) therefore thought that the capitulum of the Compositae could have been derived by further suppression of the aborted involucre flower in an inflorescence such as that of *Jasione*.

Cronquist pointed out that the Campanulaceae and the Compositae are very similar in the possession of inulin and polyacetylenes, which he considered effective against predators and therefore largely responsible for the evolutionary success of these families. He also stated, however, that the immediate ancestors of the Compositae were shrubs or small trees with opposite leaves and cymose inflorescences, thereby ruling out both the Campanulaceae (herbs, alternate leaves, mostly racemose inflorescences) and the Dipsacaceae (herbs, apical placentae).

Two of the three subfamilies of the Campanulaceae contain over 95 percent of the species; both are represented in the southeastern United States. The

Campanuloideae are readily distinguished from the Lobelioideae by their non-resupinate (vs. resupinate) flowers in which the odd petal is morphologically farthest from the axis of the inflorescence (vs. morphologically nearest but made farthest by resupination); their mostly actinomorphic (vs. zygomorphic), nonfenestrate (vs. often fenestrate) corollas; their free (vs. often connate) filaments; their coherent and eventually free (vs. connate) anthers; and their mostly three (vs. two) carpels united into an ovary with as many or (by the intrusion of false septa) more (vs. one or two) locules. The Campanuloideae (primarily herbs, rarely shrubs) consist of about 35 genera and 600 species, nearly all of which are native to the North Temperate Zone. The group is poorly represented in the Southern Hemisphere, although several small genera are endemic to South Africa, and species of (for example) *Wahlenbergia* occur in Australia, New Zealand, and South America. Conversely, the Lobelioideae (small herbs to trees) comprise about 30 genera and perhaps as many as 1200 species, approximately half of which are indigenous to South America (McVaugh, 1949b). The subfamily is otherwise worldwide in distribution, with 15 genera and many species (particularly of *Lobelia*) occurring in North America (McVaugh, 1943). The subfamily Cyphioideae (about four genera and 70 species in South Africa) is considered to be a link between the two other subfamilies in that its members usually have actinomorphic flowers, apically connate staminal filaments, and free anthers.

Genera of the Campanuloideae represented in the Southeast were placed by Schönland in three subtribes within the tribe Campanuleae. Accordingly, the Campanulinae (sepals opposite carpels, at least when equal in number to them; capsules laterally dehiscent in our species [or otherwise sometimes indehiscent, or even berries]) are represented in our area by *Campanula* and *Triodanis*; the Wahlenbergiinae Schönl. (sepals opposite carpels, at least when equal in number to them, capsules apically dehiscent in our species [or sometimes a berry]) by *Wahlenbergia* and *Jasione*; and the Platycodinae Schönl. (sepals alternate with carpels, capsules apically dehiscent in our species [sometimes laterally in others]) by *Platycodon*.^{4,5}

⁴The tribes Pentaphragmeae Schönl. and Sphenocleae Schönl. comprise the remainder of the Campanuloideae in Schönland's system. Since these are considered here to be separate families, the subtribes of Schönland would more appropriately be elevated to the rank of tribe. Therefore, Endlicher's recognition (in *Genera Plantarum*) of the Campanuleae and the Wahlenbergiae (which included *Platycodon*) is adopted here.

⁵*Platycodon* A. DC., a monotypic genus, differs from *Campanula*, in which it was placed initially, in its large flowers, broadly campanulate corollas, and apical, instead of lateral, capsule dehiscence. In contrast to *Wahlenbergia*, in which it has also been placed (and to *Campanula*, *Jasione*, and *Triodanis* as well), *Platycodon* has carpels never opposite the calyx lobes (see, however, Ohwi). The most distinctive feature of the genus is the inflated appearance of the corolla before the separation of its lobes.

Platycodon grandiflorus (Jacq.) A. DC., $2n = 16, 18, 28$ (Gadella, 1966a, counted only $2n = 18$ in many plants, considered $2n = 28$ to be erroneous, and did not mention $2n = 16$), is a native of northeastern Asia that has been reported as a waif in Warren Co., North Carolina (Radford *et al.*; I have seen one specimen from this locality). Although several species of *Platycodon* have been described, there is general agreement that these represent forms resulting from human manipulation of *P. grandiflorus*. The species is in great demand for both ornamental and medicinal purposes and has therefore been widely distributed. According to Bailey and colleagues, the plants are hardy in the

The delimitation of genera in the Campanuloideae, and in particular within the Campanulinae (here Campanuleae), is often exceedingly difficult (Gadella, 1966a; McVaugh, 1945b). Many small genera have been segregated from *Campanula*, which despite its progressively narrower circumscription remains of doubtful homogeneity. There is, however, little reason for confusion of genera when only plants in the southeastern United States are considered.

Schönland's treatment of the Lobelioideae involved no structuring between the levels of subfamily and genus, whereas that of Wimmer included two tribes and a number of subtribes. Although both the Delisseae Reichenb. (top of the ovary flat, fruit indehiscent) and the Lobelieae (top of the ovary conical, fruit dehiscent) are represented in North America, tribes were not used by McVaugh (1943) in his treatment of the species occurring there. (For evidence that the tribes proposed by Wimmer do not merit recognition, see discussion of *Lobelia*.) Our species belong to the genus *Lobelia*.⁶

With the exception of the Cyphioideae, the Campanulaceae have become relatively well known chemically over the past 20 years. Carbohydrates are stored as the fructose- (and probably glucose-) containing polysaccharide inulin (also present in the Goodeniaceae [Cronquist]). Although such compounds are usually of limited taxonomic value, inulin was indicated by Gibbs as most likely to be universal in only two families, the Compositae (Asteraceae) and the Campanulaceae. Acetylenes have been detected in 18 dicot families (Bohlmann *et al.*). Although best represented in the Compositae, they are rather common in the Campanulaceae (e.g., *Campanula* [*C. persicifolia* L., *C. rapunculoides* L.], *Wahlenbergia* [*W. gracilis* (Forster) A. DC.], *Jasione*, *Platycodon* [*P. grandiflorus*], *Lobelia* [*L. cardinalis* L.]); they have not been reported in either the Sphenocleaceae or the Goodeniaceae. Whereas the acetylenes in the Campanulaceae are aliphatic, those in the Compositae are often aromatic. One group, the tetrahydropyranes, is evidently restricted to (and widespread in) the Campanulaceae (Bohlmann *et al.*).

The chemistry of the latex universally present in the Campanulaceae evidently differs in the two major subfamilies. Although in the Campanuloideae the latex contains polysterols and a phenolic glycoside (campanulin), its chemistry is otherwise poorly known in this group; alkaloids or other toxic substances have not been found in the Campanuloideae (Hegnauer *in* Moeliono & Tuyn). In contrast, subfam. Lobelioideae includes many species that are toxic because

North (presumably the northern United States and adjacent parts of Canada) and are adapted to sunny conditions and loamy soils. Although a number of cultivars are grown in North America, it is unclear whether *P. grandiflorus* has become naturalized anywhere on the continent.

Platyconin, an unusually stable anthocyanin based on delphinidin, has been isolated from the fresh petals of several cultivars and found not to vary among them (Saito *et al.*). *Platycodon* appears to be the only genus in the Campanulaceae that is saponiferous (Agarwal & Rastogi).

⁶According to McVaugh (1940a, 1943) the lobelioid and monotypic *Hippobroma* G. Don (included by Wimmer in *Laurentia* Adanson) is represented in the Southeast (Gulf Coast from Florida to Central America) by *H. longiflora* (L.) G. Don (*Lobelia longiflora* L.), a widely established escape from cultivation perhaps originally native to the West Indies. However, Ward contended that collections indisputably from Florida were unknown and that (as of 1978) the species did not occur in the state. According to Ward, its leaves and latex are extremely poisonous.

of alkaloids that are restricted to the latex (about 30 structurally related alkaloids have been found in *Lobelia inflata* L.). Pyridine alkaloids are present in the Lobelioideae (and in particular in a number of Southeastern species of *Lobelia*) and also in the Compositae (see primarily Hegnauer, 1954).

Ramstad was evidently the first to report phenolic compounds in the Campanulaceae. He tested over 1000 species of angiosperms in 238 genera and nine families (not including either the Sphenocleaceae or members of the Campanuloideae) for chelidonic acid and found that of 15 genera of Lobelioideae examined, eight (including ten Southeastern species of *Lobelia*) contained the compound. Bate-Smith surveyed a very large number of taxa for phenolics and found that they were more common in the Campanuloideae than in the Lobelioideae. Caffeic acid (e.g., in *Campanula*) and *p*-coumaric acid (e.g., in *Campanula* and *Jasione*), perhaps the most common phenolic compounds among angiosperms (Gibbs), have frequently been identified in members of the Campanuloideae but are apparently absent in the Lobelioideae. Quercetin and kaempferol were found in *Campanula*; ferulic acid in genera including *Campanula*, *Jasione*, and *Lobelia*; cyanidin in *Centropogon* (Lobelioideae); and sinaptic acid in *Lobelia*. Both the Compositae and the Campanulaceae are among the several families that generally lack both leucoanthocyanins and the trihydroxy constituents leucodelphinidin, myricetin, and ellagic acid.

Flavonoids in general are not especially well represented in the Campanulaceae. However, anthocyanins have been found in *Campanula* (a pelargonidin [Asen *et al.*]), in *Platycodon grandiflorus* (platyconin [Saito *et al.*]), and in *Lobelia* (a delphinidin that is possibly unique among flavonoids [Yoshitama]); campanoside, cynaroside, and luteolin have been reported in *Campanula* (Teslov, 1977a, 1977b; Teslov & Teslov; Teslov & Zapesochnaya); and luteolin has been identified in *Jasione montana* L. (Zapesochnaya *et al.*).

Cyanogenesis appears to be rare in the Campanulaceae. Gibbs reported negative results for 28 species (e.g., in *Campanula* [including *C. rapunculoides*], *Wahlenbergia*, *Jasione*, *Platycodon* [*P. grandiflorus*], and *Lobelia* [including *L. cardinalis*, *L. inflata*]). Tjon Sie Fat obtained consistently negative results for species including *Campanula persicifolia*, *C. rapunculoides*, and *Jasione montana* but detected triglochinin in several species of *Campanula*, including the extraregional and polymorphic *C. rotundifolia* L. In this species cyanogenesis is variable. Although more than half of the plants tested released HCN, others lacked either triglochinin or the enzyme necessary for its hydrolysis. The presence in the Campanulaceae of triglochinin, a tyrosine-derived cyanogenic glucoside, is notable in that such compounds in the Compositae are either valine- or phenylalanine-derived (Tjon Sie Fat; see also Saupe).

The Campanulaceae are not saponiferous (see Seigler), with the exception of *Platycodon grandiflorus* (see Agarwal & Rastogi); and they lack iridoid compounds (Gibbs; see also Jensen *et al.*). Although Bate-Smith and Metcalfe & Chalk included the Campanulaceae among families in which all species lacked tannins, Gibbs reported tannins from at least six genera of Campanuloideae and one of Lobelioideae (genera not indicated; see Moreira).

A great deal of cytological diversity exists within the Campanulaceae. Basic chromosome numbers range from $x = 5$ (probable) to $x = 17$, possibly due to

a period of fluctuation early in the history of the group (Contandriopoulos). Some genera (including *Campanula*) are extremely complex cytotaxonomically, with several base chromosome numbers, while others (including *Wahlenbergia*, *Jasione*, *Platycodon*, and *Lobelia*) appear to be monobasic.

According to Brewbaker, trinucleate pollen occurs widely in members of both major subfamilies and in *Sphenoclea* but is unknown in other members of the Campanulales (pollen of the Goodeniaceae is binucleate). Binucleate pollen occurs in genera including *Campanula*, *Jasione*, and *Platycodon*, while *Lobelia* is one of ten genera of flowering plants in which both bi- and trinucleate pollen are present (pollen of *L. cardinalis* is binucleate). Davis reported that the pollen is two celled when shed in *Campanula americana* L. and in an extraregional species of *Wahlenbergia*, but three celled in *W. gracilis*.

Pollen morphology in the Campanulaceae and related families was studied by Dunbar (1973a, 1973b, 1975a, 1975b). The exine is usually spinulose in the Campanuloideae and reticulate in the Lobelioideae, but there are exceptions. Both conditions occur in species of the extraregional campanuloid genus *Phyteuma* (Dunbar, 1973a, 1975a). In genera including *Campanula*, *Wahlenbergia*, and *Platycodon* the spinules are often divided at the base. The pollen in the family has from two to 12 apertures of various kinds that at least in *Campanula* and *Jasione* may be operculate as well. The apertures in the Campanuloideae are porate in most genera (e.g., *Campanula*, *Triodanis*, *Wahlenbergia*, *Jasione*), colporate in some (e.g., *Platycodon*), and colpate in others. Aperture type in this subfamily does not agree well with the subtribes of Schönland but is correlated with pollen shape. Porate, colporate, and colpate grains occur in the Campanulinae and Wahlenbergiinae, and both porate and colporate types are found in the Platycodinae (see also Erdtman). Porate grains are spherical to oblate-spherical, while colpate and colporate pollen is frequently prolate, increasing in equatorial width (i.e., becoming more oblate) with increasing numbers of apertures. Porate grains in the Campanuloideae are considered to have developed in connection with a migration to the temperate zones; evolution in *Campanula* involved the development of smaller spinules and increasing numbers of pores as well (Dunbar, 1975b). In the Lobelioideae colpate grains occur in *Laurentia* and *Lobelia* (Lobelieae), and colporate types occur in six other genera examined (including one genus of Delisseae). The sexine pattern and apertures of *Platycodon grandiflorus* evidently resemble those of some species of *Campanula* (including *C. persicifolia*) rather closely, indicating an affinity between these two genera (Dunbar, 1975b). Data on pollen morphology substantiate the contention that genera within the Campanuloideae remain poorly defined and that *Campanula* in particular is still rather heterogeneous, despite the segregation of many genera (Dunbar, 1975b).

Palynological evidence agrees with that provided by macromorphology regarding the intermediacy of the Cyphioideae, although according to Dunbar (1975b) it also suggests that they are more closely related to the Lobelioideae (as indicated by sexine patterning in particular). Nevertheless, Chapman concluded that these three subfamilies are poorly distinguished palynologically.

Dunbar (1975b) argued that palynologically the Campanulaceae appear to be more similar to the Goodeniaceae than to the Sphenocleaceae. The tectum of both *Cyananthus* (Campanulaceae) and *Scaevola* (Goodeniaceae) is uniformly punctate, although neither the aperture type ("lalongated os") nor the variable sexine thickness in *Scaevola* is seen in the Campanulaceae. The grains of *Sphenoclea zeylanica* have smooth surfaces (although Cronquist reported that they are reticulate), with protrusions of various sizes distributed in a pattern unlike any seen in the Campanulaceae.

The ovule in the Campanulaceae is unitegmic, anatropous, and tenuinucellar (the usually single archesporial cell becomes the megaspore mother cell, although instances of more than one archesporial cell per ovule have been reported in *Campanula* [Rosén, 1949]). The megagametophyte is of the Polygonum type and usually develops from the chalazal megaspore of a linear tetrad (Davis). However, development of nonchalazal megaspores and the occurrence of T-shaped tetrads have been observed in *Wahlenbergia* (Subramanyam, 1948). The synergids are hooked in *Wahlenbergia* and other genera (Subramanyam, 1948), and a filiform apparatus has been reported in *Campanula* (Barnes) and *Lobelia* (Davis). Of the 295 families for which such information is available, 56 demonstrated both of these characters. Nevertheless, neither occurs throughout a given family, suggesting that their taxonomic significance may lie below this level (Davis). Starch grains are present in the embryo sac of *Campanula* and *Wahlenbergia*, among others (Davis).

Endosperm formation is *ab initio* cellular, although its development is of three different types (Rosén, 1949): Codonopsis type (e.g., in *Campanula*, *Wahlenbergia*, *Lobelia*), Phyteuma type (e.g., in *Campanula*, *Triodanis*, *Laurentia* [Lobelioideae]), and Sphenoclea type (in *Sphenoclea*). (It is notable that the Phyteuma type was considered transitional to a fourth type, found in the Goodeniaceae.) Both micropylar and chalazal haustoria occur throughout the family, as does the Solanad type of embryogeny (Davis). Polyembryony has been observed in *Jasione*, *Wahlenbergia*, *Lobelia*, and others. The seeds are small and exarillate. According to Corner, the exotestae are composed either of cuboid or fibriform cells, although the taxonomic significance of this in the Campanulaceae was not indicated.

The economic significance of the Campanulaceae lies chiefly in its relatively large number of attractive ornamentals. Species of many genera, including all those represented in the Southeast, are often favored by gardeners (see Bailey *et al.*, Bailey & Lawrence, Crook). A number of species, particularly of *Lobelia*, have been of medicinal and/or other value as well (see discussions and bibliographies of genera).

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KEY TO THE GENERA OF CAMPANULACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *herbs with latex; leaves simple, usually alternate, exstipulate, sessile to petiolate, margins various, sometimes lobed; flowers in inflorescences (rarely only 1 or a few per plant), perfect, sometimes cleistogamous, often showy, sometimes bracteolate, actinomorphic or zygomorphic, proterandrous; hypanthium sometimes extended above ovary; calyx synsepalous, usually 5-lobed (often with a reflexed appendage in the sinuses between lobes), persistent in fruit; corolla sympetalous, lobes usually 5 and alternate with the calyx lobes; stamens equal in number to and alternate with the corolla lobes, filaments sometimes connate above, anthers forming a tube (either by coherence or connation) into which pollen is shed and from which the pollen is removed by elongation of the style; gynoecium usually 2- or 3-carpellate, syncarpous, ovary inferior or half-inferior and often bearing an annular nectariferous disc, the locules usually equal in number to the carpels; ovules numerous in each locule on mostly axile placentae, anatropous, unitegmic; fruit a capsule, dehiscent apically or laterally; seeds numerous, small.*

- A. Corollas actinomorphic or nearly so; anthers free or coherent in a tube around the style, becoming free after anthesis; staminal filaments free; carpels usually 3; flowers not resupinate.
- B. Capsules dehiscent apically (within the calyx lobes); flowers solitary (or nearly so), in compact umbels, or in open inflorescences (and leaves then sessile and at least the lower ones entire, undulate, and/or remotely and finely serrate; anthers free and caducous; styles not conspicuously exerted).
- C. Flowers/fruits in an (involucrate) umbel. 4. *Jasione*.
- C. Flowers/fruits not in an umbel.
- D. Flowers small, numerous, arranged in an open inflorescence; plants often much branched (sometimes from the base); leaves small, linear to narrowly elliptic, if serrate only remotely and finely so. 3. *Wahlenbergia*.
- D. Flowers large, 1 to few, solitary or nearly so; plants often unbranched (never branched from the base); leaves large, ovate to elliptic, serrate. [Platycodon; see footnote 5.]
- B. Capsules dehiscent laterally; flowers in spikes or in open inflorescences (and most leaves then petiolate or at least constricted at base and at least lower ones coarsely serrate, very rarely remotely and finely serrate; anthers coherent and persistent; styles conspicuously exerted).
- E. Inflorescence branched, or if spicate the flowers pedicellate, corollas campanulate, or if rotate the styles upcurved; leaves usually petiolate; cleistogamous flowers lacking; capsules obconical to subglobose. . . . 1. *Campanula*.
- E. Inflorescence spicate, flowers sessile, corollas rotate, styles straight; leaves sessile; cleistogamous flowers present (at lower nodes); capsules narrowly cylindrical. 2. *Triodanis*.
- A. Corollas zygomorphic; anthers connate in a tube around the style, not becoming free after anthesis; staminal filaments connate above; carpels 2; flowers resupinate. 5. *Lobelia*.

Subfam. CAMPANULOIDEAE [Schönland, Nat. Pflanzenfam. IV. 5: 48. 1889]

Tribe CAMPANULEAE [Endlicher, Gen. Pl. 516. 1838]

1. **Campanula** Linnaeus, Sp. Pl. 1: 163. 1753; Gen. Pl. ed. 5. 77. 1754.

Erect, suberect [or rosette- or mat-forming], perennial or sometimes annual [or biennial] herbs. Leaves alternate, sessile to petiolate, entire or dentate, sometimes lobed. Inflorescences racemes or panicles, sometimes spikes [or heads, or flowers solitary]; flowers perfect. Calyx actinomorphic, the tube ovoid or subglobose, 5-lobed, needle shaped to triangular, often with a reflexed lobe or appendage in each sinus, commonly longer than the tube. Corolla actinomorphic, rotate, campanulate, or funnelform, lobes 5. Stamens 5, epipetalous; filament strongly to weakly dilated at the often-persistent base; anther elongate. Ovary inferior, locules 3–5; placentation axile; stigma lobes 3–5. Fruit an ovoid to turbinate capsule, often strongly ribbed, dehiscent by 3–5 lateral pores or valves [rarely indehiscent]; seeds brown, lustrous, ellipsoid, turgid or flattened. (Including *Rotantha* J. K. Small, 1933, not J. G. Baker, 1890, and *Campanulastrum* J. K. Small, 1903.) LECTOTYPE SPECIES: *C. latifolia* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. 3: 294. 1913. (*Campanula* listed by Linnaeus [Philosophia Botanica, p. 142. 1737] as a name provided by Tournefort. Name from Latin *campana*, a bell, referring to the shape of the corolla, and *ula*, diminutive.)—BELLFLOWER.

The largest genus in the Campanuloideae, consisting of over 300 species (more than 500, according to Contandriopoulos) and mostly confined to the North Temperate Zone. The plants occupy a variety of habitats (e.g., deserts, forests) but are most frequent and most diverse at high elevations. Relatively large numbers of species occur in the Caucasus and eastern Mediterranean regions, as well as in the mountains of western Europe. There are about 150 species in the Soviet Union (Fedorov) and some 144 in Europe (Fedorov & Kovanda in Tutin). About 20 species are native to North America (Shetler, 1963).

Despite the segregation of a number of genera (including *Platycodon* and *Triodanis*) from *Campanula*, doubts regarding its homogeneity persist. In addition, although most species of *Campanula* are fairly well marked, infrageneric relationships (i.e., species groupings) are obscure. Two initial classifications (A. de Candolle, Boissier) were rather conflicting, and although each has been shown to be mostly unnatural, no modern alternatives based on world-wide study have been published. It is almost universally agreed among students of the group that a modern revision is long overdue; most investigators have indicated that a successful treatment must incorporate cytology, seed morphology, capsule dehiscence, life form, and geography.

Alphonse de Candolle divided *Campanula* into two sections based on the presence (sect. *Medium* A. DC.) or absence (sect. *Eucodon* A. DC. [= sect. *Campanula*]) of appendages between the calyx lobes. Although his treatment is still of value (it is the only treatment on a worldwide basis), species that do not fit in either section have subsequently been described. Boissier considered the nature of capsule dehiscence to be of greater taxonomic value, and on that basis he proposed two sections with different circumscriptions. Species in De Candolle's sect. *Eucodon* with dehiscence near the top of the capsule were removed to sect. *Rapunculus* Boiss., while the remaining species (including the type of the genus) were united with sect. *Medium* A. DC. to form a group in which dehiscence was basal. Most subsequent treatments, including that of Schönland, have followed the system of Boissier, even though it is generally regarded to be as artificial as that of De Candolle. In the *Flora of the U.S.S.R.*, Fedorov recognized the two sections of Boissier but further divided them into subsections and series that are in most cases more natural than the sections. Damboldt's treatment for the *Flora of Turkey* largely follows that of Fedorov, except that many of Fedorov's infrageneric taxa are elevated in rank. (Damboldt recognized six subgenera and numerous sections.)

Numerous cytological studies have provided data bearing on the infrageneric relationships of *Campanula*. Sugiura concluded from evidence obtained from over 70 species that the genus is composed of two main groups. Those species with a gametic chromosome number of eight (or some multiple of eight) evidently have linear-lanceolate leaves, while those with 17 (or some multiple of 17) have wider leaves.

Gadella (1964) showed that De Candolle's sect. *Medium* is rather homogeneous cytologically: 19 of 21 species with appendaged calyces have $2n = 34$, although many (but not all) of the exappendiculate species comprising De

Candolle's sect. *Eucodon* were also found to be of this cytotype. Boissier's sections, on the other hand, were considered to be cytologically heterogeneous. Sugiura's proposal of two groups differing in base chromosome number and leaf shape was regarded as untenable by Gadella, who (for reasons that do not appear to be completely justified) indicated instead that a classification based on a combination of characters, including chromosome length and base number, basal leaf shape, and location of capsule dehiscence, seemed justified. Accordingly, Gadella established seven informal groups of species that differ in base chromosome numbers. Since a majority of the species of *Campanula* were not considered and the relationships involved were unclear, the arrangement was considered provisional.

The chromosome numbers characterizing some of Gadella's groups have been determined subsequently in more distantly related species; in some cases the same number has been differently and independently derived as well. Nevertheless, Contandriopoulos considered Gadella's approach to be well founded and proposed a phylogeny based on cytology, morphology, life cycle, and geographic distribution that reflected the exceedingly complex cytotaxonomy of *Campanula* and suggested how Gadella's groups might be interrelated. The base chromosome numbers 5, 6, 7, 8, and 9 were considered to be primary; 8 was thought to be the ancestral number, perhaps evolved independently of 9 but more directly linked to the others. A secondary base number, 17, is characteristic of a great many species in the genus (and in the family as well—several genera have only species with this number). Contandriopoulos rejected the idea that $x = 17$ resulted from amphiploidy involving plants with either $x = 7$ and $x = 10$ or $x = 8$ and $x = 9$ and accepted as plausible the hypothesis of Böcher (1960), who considered 17 to have resulted from a single trisomy in the $2n = 16$ cytotype (see, however, Sugiura; Gadella, 1963, 1964).

Fedorov's classification of *Campanula* is usually considered to be the most natural, apart from the questionable division of the genus into two sections based on the location of capsule dehiscence. Gadella (1964) regarded it as artificial only for those subsections between which members had been successfully hybridized (by him). Since only two of our species, both naturalized in the Southeast, are from the Old World, application of Fedorov's system to the others is unclear. With the possible exception of *C. Robinsiae* Small, the species indigenous to our area are restricted to North America and are probably unrelated to any in the Old World.

The most recent enumeration of the North American species of *Campanula* was provided by Shetler (1963). Of the 20 native species, 16 were indicated to be endemic to a portion of the continent, two were amphi-Atlantic, and two were circumpolar. Three European species (excluding *C. persicifolia* L., below) were considered to have escaped from cultivation and to have become naturalized in (unnamed parts of) North America.

Three or four species (depending on taxonomic interpretation) of *Campanula* are indigenous in the Southeast, while the origin of *C. Robinsiae* has yet to be resolved.

Campanula Robinsiae differs from other species of the southeastern United States, with the exception of the very distinctive *C. americana* L., in its annual habit. Although initially considered to be endemic to a small area in Florida, its status at present is uncertain. The area in which it occurs—wet, grassy slopes of Chinsegut Hill, near Brooksville, Hernando Co., Florida, an area long disturbed by cultivation—is not especially known for local endemics (Shetler, 1963). Its similarity to *C. Reverchonii* Gray, an annual species endemic to granitic soil in the Llano region of the Edwards Plateau in Texas, was noted by Small (1926) and by Shetler (1963). However, Ward pointed out that such a distribution is not duplicated by other species pairs and summarized arguments that *C. Robinsiae* most likely represents a recent introduction from the Old World. Morin (pers. comm.) recently collected *C. Robinsiae* from wet places in the Brooksville area (some plants submerged). She considered it to be unrelated to any other North American species of *Campanula*, in part because in her material the pollen had bifurcate spines on the surface and the seeds in cross section were triangular with protuberances on the angles. The annual habit, the low, divaricately branched, leafy stems, the absence of rosettes, and the basal capsule dehiscence suggest to me that its affinities may lie with species belonging to subsect. *Annuae* (Boiss.) Fedorov and native to the Caucasus and Mediterranean regions.

Campanula aparinoides Pursh, $2n = 34, 136, 170$, and *C. floridana* S. Watson ex Gray are closely related. Indeed, Shetler (1963) recognized the possibility that *C. floridana*, an endemic of peninsular Florida, is merely a southern race of the more widespread *C. aparinoides*, which has not been recognized in Florida but is found in the northeastern part of our range. Both are plants of swamps, marshes, and peatlands and have weak, slender, reclining stems—features that separate them from all other southeastern species of *Campanula*. *Campanula aparinoides* differs from *C. floridana* in its (usually) retrorsely scabrous stems and leaves and its campanulate or funnelform (vs. more rotate) corollas that are rarely divided below the middle (vs. divided almost to the base) into wide (vs. narrow) lobes. *Campanula aparinoides* is generally considered to be endemic to the eastern and central United States and adjacent Canada but has recently been reported from Wyoming, apparently as a native (Lichvar & Dorn). The position of these species in Fedorov's system is not clear, although A. de Candolle included *C. aparinoides* (and *C. divaricata*, below) in a group of 22 species that also included *C. rotundifolia* L., $2n = 68$, a species placed by Fedorov in subsect. *Heterophylla* (cited as subsect. *Heterophylla* (Nyman) Fedorov by Fedorov; see, however, Geslot) (flowers drooping, calyces exappendiculate, capsules dehiscing at the base). *Campanula aparinoides* qualifies on cytological grounds for inclusion in Gadella's group VII, a heterogeneous assemblage that included species in many of Fedorov's subsections, including subsect. *Heterophylla*. Among the indigenous species of *Campanula* in the Southeast, *C. aparinoides* may bear a relationship to *C. rapunculoides* L., $2n = 68, 102$, of subsect. *Campanula* (stems tall, simple; inflorescences many flowered, racemose; calyces exappendiculate; capsules pendulous, dehiscing near the base). Although *C. floridana* and *C. Robinsiae* were placed by Small in his genus *Rotantha*, the species are clearly unrelated.

Campanula divaricata Michaux (*C. flexuosa* Michaux⁷), $2n = 40$ (34 according to Gadella, 1964), is an erect plant with profusely branched panicles, small, shallowly incised corollas with recurved lobes, and conspicuously exerted styles. It generally occurs at low elevations in the Appalachians, on cliffs (often in small crevices), in dry rocky woods, and along waysides. Endemic to an area from Maryland south to Georgia and Alabama, it rarely is an adventive farther north (Shetler, 1963). Pease reported that a single individual persisted naturally in New Hampshire at least from 1920 to 1960 without reproducing sexually. *Campanula divaricata*, like most other North American endemics in the genus, is largely confined to unglaciated regions. It is therefore thought to have survived south of the limit of glaciation. Contandriopoulos indicated that species with $2n = 40$ belong to a lineage with $x = 5$ as the base number. This lineage appears to be monophyletic and unrelated to other lines, including those to which other southeastern species belong.

According to Shetler (1958) *Campanula americana* L., $2n = 58, 102$, has no close relatives in the genus. Its tall, robust habit, rotate, deeply cut corollas, and exerted, upcurved styles represent a unique combination of characters within the genus. Nevertheless, its separation by Small into the monotypic *Campanulastrum* was not initially supported by Shetler (1958; see, however, Shetler & Matthews) because the rotate corollas at least in part defining this genus do not occur in *C. americana* f. *tubulifera* Fern. and are found elsewhere in *Campanula*.⁸ Shetler & Matthews favored recognition of *Campanulastrum* on cytological and palynological evidence, as did Gadella (1964, 1966b) on cytological and morphological grounds.

Shetler (1958) observed that plants of *Campanula Scouleri* Hooker, of the west coast of North America (Alaskan panhandle to northern California), are very similar to small, unbranched individuals of *C. americana* and suggested that the latter may represent diploids in a series in which larger, more typical plants are polyploids ($2n = 102$). However, Gadella (1964) reported a diploid number of 58 throughout *C. americana*, and the chromosome number of *C. Scouleri* has not been reported.

There has been some confusion about the duration of individuals of *Campanula americana*. The species has been reported as an annual (Cruden; Senior; Shetler, 1962; Steyermark), a biennial (Morin; Radford *et al.*; Shetler, 1963), or as an annual or biennial (Diggs; Small, 1933). Baskin & Baskin studied populations in an open secondary hardwood-*Juniperus virginiana* forest in Kentucky (Fayette Co.) and found a low-temperature vernalization requirement for flowering that could not be met in the seed stage. Since *C. americana* is monocarpic, it behaves either as a winter annual, if plants are from seeds that germinated in summer or fall, or as a biennial, if the seeds germinated in spring. The Baskins concluded that a relatively simple genetic change could result in

⁷Gray (Synopt. Fl. N. Am. 2: 13, 14. 1878) was evidently the first to unite these species. His choice of *Campanula divaricata* must be followed in accordance with Article 57.2, ICBN, 1983.

⁸As Shetler (1958) has pointed out, Small must have had other characters in mind when he established the genus *Campanulastrum*, or he presumably would not have later erected the genus *Rotantha* for two other species with rotate corollas, *C. floridana* and *C. Robinsiae*.

a shift from one to the other life cycle, and that plants of the species may indeed behave differently in different populations.

Campanula americana is endemic to and widely distributed throughout eastern North America, where it occurs in partial shade in moist, rich, well-drained, usually calcareous soil. Although it is most common near streams and rivers, it is not restricted to alluvial conditions (Shetler, 1958). It evidently occurs throughout the Southeast, but its abundance appears to be correlated positively with elevation. It is clearly least frequent on the Coastal Plain and is less abundant in the Piedmont than in the adjacent mountains. In Florida it is restricted to the western part (the panhandle).

Fedorov included *Campanula persicifolia* L. and *C. Rapunculus* in subsect. *Campanulastrum* (Small) Fedorov. However, his designation of *C. Rapunculus* as the type of this subsection is incorrect because *C. americana* was the only species included in the genus *Campanulastrum* by Small and must, therefore, be considered the type. *Campanula americana* does not appear to belong to the group of Russian plants recognized by Fedorov.

Campanula rapunculoides, $2n = 68, 102$, is similar to *C. americana* in its coarse, erect habit and spicate inflorescences, but it differs in its secund inflorescences, campanulate to tubular corollas (rarely incised below the middle), included or barely exerted and never upcurved styles, and basal capsule dehiscence (vs. dehiscence near the top of the capsule). A native of Eurasia, *C. rapunculoides* is widely naturalized as an escape from cultivation. It occurs throughout the northeastern quarter of the United States and adjacent Canada (Newfoundland to North Dakota south to Maryland and Illinois) along roadsides and in waste-ground and yards. It is rare and of restricted distribution in the Southeast, where it is known with certainty only from Watauga and Avery counties in northwestern North Carolina. It is known from two counties in northern Missouri (Steyermark) and from one in southwestern Virginia, as well. In the southern part of its indigenous Old World range, *C. rapunculoides* has diverged into a series of intergrading races, but it is more uniform toward its northern limit at the forest-tundra ecotone (Fedorov). *Campanula rapunculoides* was placed by Fedorov in subsect. *Eucodon* (= subsect. *Campanula*) ser. *Rapunculoideae* Charadze, which differs from ser. *Latifoliae* (= ser. *Campanula*) in its smaller flowers and its curved or spreading (vs. straight) calyx lobes that are $\frac{1}{5}$ to $\frac{1}{4}$ (vs. $\frac{1}{3}$ to $\frac{1}{2}$) as long as the corolla. Damboldt put *C. rapunculoides* in sect. *Quinqueloculares* (Boiss.) Phitos. Its possible relationship to *C. aparinoides* is discussed above.

Campanula persicifolia L., $2n = 16$ (some 17, 18, 32), superficially resembles *C. rapunculoides* but has narrower cauline leaves and more deeply trifid styles. A native of Europe, it has been reported as an escape from cultivation in North America in both western North Carolina (Small, 1933; but specimens substantiating this have not been located) and eastern Canada, where it is reportedly naturalized as well (Cinq-Mars *et al.*). Morin (pers. comm.) noted a specimen from Nebraska in the collections of the Missouri Botanical Garden, but neither she nor I have seen any material from the Southeast. The species was placed by Fedorov in subsect. *Campanulastrum* and by Gadella (1964) in his Group I. According to the scheme of Contandriopoulos, it is unrelated to other species

occurring in the Southeast. Artificial hybrids between *C. persicifolia* and the closely related *C. latiloba* DC. were sterile (Gadella, 1967).

The apparent absence from the Southeast of the extremely polymorphic and circumboreal *Campanula rotundifolia* L. is somewhat surprising, since it occurs throughout North America, with the most notable exception of the extreme Southwest and our area (Shetler, 1979b). It grows in Missouri in moist, shaded, north-facing crevices of limestone in the southeastern Ozarks (Shannon Co.) within about 40 miles of Arkansas (Steyermark), as well as in western Texas and parts of Mexico (Shetler, 1979b).

Pollen in *Campanula* is binucleate when shed (Brewbaker). It is generally spherical to suboblate (occasionally subprolate) and has three or four usually equatorial pores. Usually the surface bears spines that vary in size (particularly between species) and are superimposed on a fine reticulum. It is notable that pollen of *C. americana* has 12 pores distributed more or less equally over the entire surface of the grain and that in sexine pattern it is similar to that of *Wahlenbergia* and certain other genera of the Campanulaceae (Dunbar, 1975b).

An extensive literature dealing with the reproductive biology of *Campanula*, including a debate concerning the relative importance of autogamy in the genus, has been thoroughly reviewed by Shetler (1979a). Species of *Campanula* were often thought not to be insect pollinated and/or not to be allogamous, primarily because of the way in which the pollen is presented. While the flower is still in bud, the coherent anthers begin to shed pollen introrsely onto retractile hairs on the apical portion of the style. During anthesis pollen is carried aloft out of the anther tube as the base of the style elongates; the stigmas do not normally spread until all of the hairs and pollen grains have disappeared from the style. Nevertheless, the deposition of pollen on the style and the retraction of the trichomes have often been thought to constitute self pollination and to lead to self fertilization by growth of pollen tubes directly into the style. Other arguments for autogamy have pointed out that pollen release and stigma receptivity sometimes overlap in individual flowers (and that in such cases exiting insects could transport pollen from style to stigma), that pollen could fall from styles to stigmas in pendent flowers, and that recurving stigmas could eventually come in contact with the style. Autogamy could also be effected by insects in multiflowered species, since floral development is sequential. Despite these and other hypotheses that have generally not been supported by observation, most evidence indicates that cross pollination (and subsequent fertilization) by insects is the rule within the genus. (For a list of pollinators, see Knuth.)

The flowers of *Campanula* show adaptations usually associated with insect pollination, including blue or violet, campanulate or tubular corollas; nectar and a means of protecting it from visitors that do not enter the flower in a way likely to effect pollination (the broad, triangular filament bases form a dome over the nectary such that entrance to it can best be gained near the style after passage by pollen and stigma); proterandry; and echinate pollen. Gadella (1964) found that among 21 species tested, spontaneous self fertilization occurred in only two (including one population of *C. persicifolia*) when flowers were bagged, and that mature seeds were produced in only one of 18 species artificially self pollinated.

Narrower debates have centered on the adaptive significance of the method of pollen presentation in *Campanula*, and in particular on the fact that the collecting hairs retract. The mechanism of presentation may prevent pollen gathering by nonpollinating visitors, and/or it may insure that pollen is deposited on pollinators in places most likely to come in contact with stigmas of the same species, thus contributing to pollen economy and perhaps to reproductive isolation as well (Brantjes). It seems clear that the hairs serve to hold the pollen in place as it is removed from the anther tube, but it has been suggested that they may also help in the exit of small insects from the corolla.

The retraction of the collecting hairs, a feature probably unique to the Campanulaceae, involves an invagination of the apical portion of each hair into its basal portion that is thought to be irreversible and osmotically induced (see Shetler, 1979a). Although this may be a mechanism by which pollen is brought into contact with the stylar tissue, it has been shown that the hairs do not function in this way and that pollen tubes are only able to penetrate the style through the stigmatic surfaces. The lack of evidence for spontaneous autogamy also argues against stylar pollination and, therefore, against the proposal that retracting hairs help to bring it about.

Retraction of the collecting hairs is not likely to facilitate pollen release to visiting insects and does not result from mechanical stimulation (but see Carolin, 1960), although pollen removal and hair retraction are simultaneous and do not occur to any great extent in the absence of insect visitors. Nevertheless, the hairs probably enhance the likelihood of pollination by holding pollen on the style in the path of nectar-seeking visitors. Retraction, therefore, may be of no real significance, but simply the consequence of some physiological change perhaps brought about by the pollinator.

Many species of *Campanula*, especially those with large flowers (e.g., *C. americana*, *C. persicifolia*, *C. rapunculoides*), are cultivated for their ornamental value, and some, including *C. americana*, have been investigated as sources of latex in the production of rubber (Buchanan *et al.*, 1978a, 1978b).

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2. *Triodanis* Rafinesque, *New Fl. Bot. N. Am.* **4**: 67. 1838.⁹

Erect or ascending (sometimes reclining), terrestrial, annual herbs. Stems simple to much branched, usually at or near the base; when pubescent the trichomes nonglandular, often retrorse, and largely confined to membranaceous, longitudinal ridges. Leaves alternate, often ciliate, sessile or sometimes

⁹Barnhart (*Torreyia* **7**: 177–182. 1907) showed that the publication date of this work was 1838, not 1836 as the cover indicates.

petiolate near base of plant; blade broadly ovate, elliptic, or linear, the base attenuate, cuneate, obtuse, truncate, or auriculate, sometimes clasping the stem, the apex acuminate to obtuse, sometimes mucronate, the margin entire or crenate, each tooth strongly asymmetric and often mucronate. Inflorescences appearing loosely spicate, with lower flowers usually cleistogamous (and then often with missing or rudimentary parts). Flowers sessile, actinomorphic, usually 1 per axil and terminating a repressed axillary branch [or more numerous (2 or 3, rarely to 8) when the axillary branch elongates (and sometimes branches)], sometimes subtended by a bract. Calyx actinomorphic; tube ellipsoid to narrowly ellipsoid; lobes usually 5, but sometimes 3 or 4 in cleistogamous flowers, entire, usually ciliate, attenuate, persistent in fruit. Corolla actinomorphic; tube funnellform; lobes usually 5, longer than the tube, usually about twice as long as wide, lanceolate to elliptic [or broadly ovate and abruptly acuminate], apex obtuse or attenuate. Stamens usually 5, epipetalous, rudimentary in cleistogamous flowers; filament short, flattened; anther linear, longer than the filament. Ovary inferior, locules 3 (sometimes 2; 1 in *T. leptocarpa*); placentation axile to subparietal (sometimes in individual ovaries) (parietal in *T. leptocarpa*); style rudimentary in cleistogamous flowers; stigma lobes equal in number to the locules. Fruit an ellipsoid to narrowly ellipsoid, sometimes clavate capsule (subulate in the cleistogamous flowers of *T. leptocarpa*), dehiscent by lateral pores equal in number to the locules of the ovary (except sometimes in *T. leptocarpa*); seeds mostly tan or dark brown, usually longer than wide, turgid or flattened, essentially smooth. (Excluding *Specularia* Heister ex A. DC., 1830, = *Legousia* J. F. Durande, 1782.) LECTOTYPE SPECIES: *T. rupestris* Raf. (= *T. perfoliata* (L.) Nieuwl.); see McVaugh, *Wrightia* 1: 23. 1945. (According to Rafinesque, the name means "three unequal teeth," in reference to the calyx lobes [which in fact are only sometimes unequal].)

A small genus of perhaps six or seven North American and one Mediterranean–Middle Eastern species that has gained acceptance only in relatively recent times. *Specularia* Heister ex A. DC. (= *Legousia* J. F. Durande), a group of about seven species segregated primarily from *Campanula*, was generally recognized until McVaugh (1945b) pointed out that it could not in its traditional circumscription be logically maintained apart from *Campanula*. McVaugh proposed, however, that if *Specularia* were restricted to the type (and perhaps one other species), and if the intermediate *S. pentagonia* (L.) A. DC. were transferred from *Specularia* to *Campanula*, relatively homogeneous units, including *Triodanis*, would result. Although Fernald rejected this arrangement and chose to retain *Specularia*, maintaining that there were too many qualifications to the generic differences enumerated by McVaugh, he did not address McVaugh's main argument (i.e., that if *Specularia* were segregated from *Campanula*, *Triodanis* must also be). McVaugh's rebuttal (1948) further strengthened his case, and *Triodanis* is recognized here. A combination of characters (including annual habit, deeply divided corolla, capsules that are longer than wide and open near the apex [but see below], spicate inflorescences, and regular production of cleistogamous flowers at the lower nodes) is unique and defines *Triodanis* in the sense of McVaugh (1945b).

Four or five species of *Triodanis* occur in the Southeast. *Triodanis perfoliata*

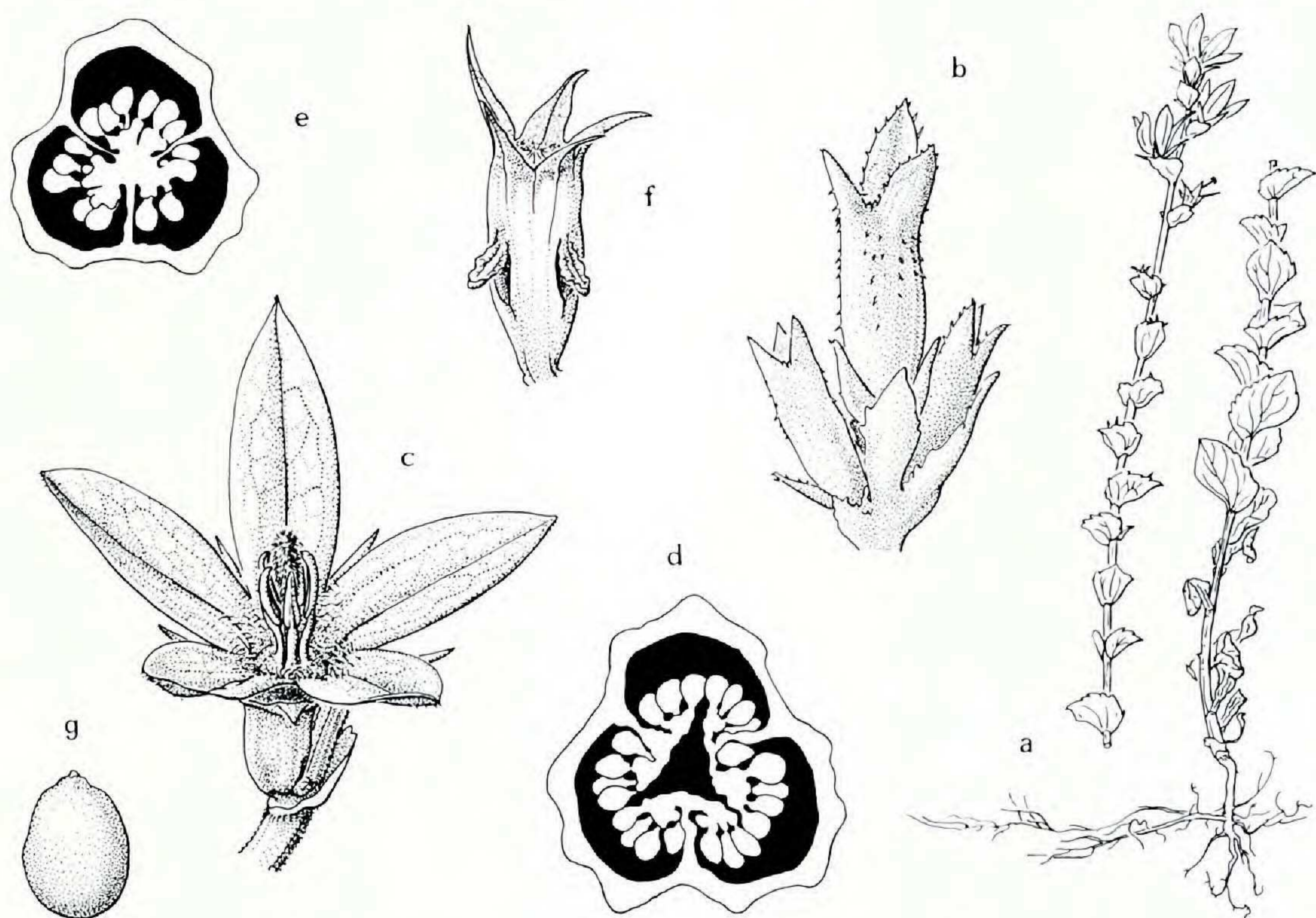


FIGURE 1. *Triodanis*. a-g, *T. perfoliata*: a, small plant, inflorescences in leaf axils appearing single flowered, $\times \frac{1}{2}$; b, axillary inflorescence with 3 cleistogamous flowers visible, each with 3 calyx lobes, the largest flower with 2 bracteoles visible, $\times 8$; c, chasmogamous flower with subtending bract removed, $\times 4$; d, cross section through apical portion of ovary (placentation intermediate between axile and parietal, the latter characteristic of *T. leptocarpa*), $\times 15$; e, cross section through basal portion of ovary, $\times 15$; f, capsule with persistent calyx lobes, lateral dehiscence, $\times 4$; g, seed, $\times 30$.

(L.) Nieuwl. (*Specularia perfoliata* (L.) A. DC.) and *T. biflora* (Ruiz & Pavon) Greene (*Specularia biflora* (Ruiz & Pavon) Fischer & Meyer), each $2n = 56$, are quite similar morphologically and may be conspecific (see below). The most common species of the genus in our area, *T. perfoliata* has—as compared with *T. biflora*—dehiscence near or below the middle of the capsule (vs. near the top), bracts that are wider than long (vs. longer than wide), and several (vs. one or two) inflorescences with chasmogamous flowers. Both species are widespread in the Southeast, although in North America *T. biflora* appears to have a more southerly distribution. It is therefore interesting that, although McVaugh (1945b) considered *T. biflora* to be native in many parts of South America, he suggested that *T. perfoliata* may have been introduced there (except perhaps in Ecuador, where it may be native). Both species occur in a variety of natural and disturbed habitats, with the exception of deserts and places with permanently wet ground. McVaugh (1943) considered *T. perfoliata* to be more abundant and to behave more like a native species than *T. biflora* on granitic flat rocks in the Southeast.

Triodanis lamprosperma McVaugh, *T. texana* McVaugh, and *T. Holzingeri* McVaugh are very similar in general appearance to the two preceding species. *Triodanis lamprosperma* is easily distinguished by its large (greater than 0.8

mm wide), flatly lenticular, smooth, highly polished seeds. It occurs in a variety of habitats in Louisiana, western Arkansas, southern Missouri, and eastern Oklahoma. *Triodanis texana*, with quadrangular, roughened seeds, occurs mostly in sandy soils in woods, pinelands, and plains and has a distribution in eastern Texas that closely approaches southwestern Louisiana. (It is evidently unknown from our area.) *Triodanis Holzingeri*, distinguished from the preceding species by linear (vs. broadly elliptic to rounded) capsule openings, occurs in prairies in the central United States. Although McVaugh (1945b) reported an outlying station in southwestern Tennessee, I have seen no specimens of this species from the Southeast.

Triodanis leptocarpa (Nutt.) Nieuwl. is easily recognized by its lanceolate to linear leaves subtending the axillary inflorescences (often appearing as flower bracts in the case of one-flowered inflorescences) and its long, narrow capsules with openings near the top. It is a prairie plant of the central United States that enters our area in western Arkansas and Louisiana. *Bradley 3281* (NY), from a roadside in Missouri, is intermediate between *T. leptocarpa* and *T. perfoliata* in the shape of leaves subtending inflorescences and in the position of capsule openings.

Cytological evidence supports the recognition of *Triodanis* (Gadella, 1966b) in that both *Specularia speculum* A. DC. (the type of *Specularia*) and *S. pentagonia* (L.) A. DC. (an enigmatic species returned to *Campanula* by McVaugh [1945b]) are $2n = 20$, while *Triodanis falcata* (Ten.) McVaugh (Mediterranean region) is $2n = 26$ and *T. perfoliata* and *T. biflora* are $2n = 56$. These data also suggest that two infrageneric taxa may be recognizable in *Triodanis*, one comprising *T. falcata* and the other made up of the New World species.

Gray proposed that the American species of *Triodanis* were divisible into two sections based primarily on placentation and capsule shape. Accordingly, he placed *T. biflora* (placentation axile, capsules elliptic) in one and *T. leptocarpa* (placentation parietal, capsules narrowly elliptic) in the other. It is notable that in *T. perfoliata* placentation in a single ovary may grade from nearly parietal in the upper part to axile toward the base (FIGURE 1d, e), suggesting that the proposed sections of Gray are untenable.

Bradley scored individuals of *Triodanis perfoliata* and *T. biflora* obtained from natural populations in the Southeast and grown under uniform conditions, as well as the offspring resulting from various crosses involving these plants (selfing, F_1 and F_2 hybrids, and backcrosses to both parents), for each of the characters mentioned above. Since a range of values extending from one extreme to the other was obtained for each character and since the hybrids were fertile, Bradley considered the plants involved to be conspecific. However, because of the persistence, despite interbreeding, of the combination of three traits characterizing *T. biflora* (which Bradley attributed to linkage and the high degree of self fertilization resulting from low numbers of chasmogamous flowers), he chose to recognize this taxon as *T. perfoliata* var. *biflora* (Ruiz & Pavon) Bradley. Ward, however, rejected this view and chose instead to maintain the species as distinct because other workers had not expressed difficulty in separating them and because his own observations revealed few or no intermediates. Ward also indicated that isolating mechanisms were clearly op-

erating in the field and that treating these taxa as varieties would constitute too great an expansion of the original meaning of that rank.

The inflorescence characters discussed above have been found to be susceptible to environmental modification. Data obtained by Trent (1940b) for *Triodanis perfoliata* indicated that, although cleistogamous and chasmogamous flowers increased in number at equal rates with increasing photoperiod, chasmogamous flowers increased more quickly than cleistogamous ones with increasing light intensity. Since in both cases cleistogamous flowers outnumbered chasmogamous ones, the proportion of all flowers that were chasmogamous was greater when both photoperiod and light intensity were increased. Bradley reported that while the number of chasmogamous inflorescences in *T. perfoliata* could be reduced to two by poor habitat conditions, *T. biflora* produced only two even under good conditions.

The structure of the flower in *Triodanis perfoliata* is extremely variable (Trent, 1940a). Among chasmogamous flowers sepals, petals, and stamens vary in number (two to seven sepals, one to six petals, and one to six stamens) and include both normal and vestigial parts, while the ovary is consistently three-locular. Cleistogamous flowers are less variable (three to six sepals, three to five petals, and one to five stamens), with sepals always normal, petals always vestigial, and stamens either normal or vestigial; the ovary is either two- or three-locular.

Trent (1942) compared the anatomy of cleistogamous and chasmogamous flowers of *Triodanis perfoliata*. The ovules and seeds of both were found to conform to the types seen throughout the Campanulaceae, although chasmogamous flowers were determined in general to produce more ovules (80–290) than cleistogamous ones (31–180). Each type of flower was found to produce both binucleate and (less frequently) trinucleate pollen, but differences in pollination were reported. Fertilization was observed in chasmogamous flowers in a few instances but never in cleistogamous ones, in which some evidence for parthenogenesis was reported (pollen grains were observed to germinate within the anthers and to grow through the anther wall but only as far as the adjacent stigma). Although embryo development in *T. perfoliata* appeared to conform to the “*Capsella* type” (= Crucifer type?), something closer to what is usually termed the Solanad type (characteristic of the Campanulaceae) was described (the basal cell results in a suspensor of 5 or 6 cells). Triple fusion may or may not occur, and endosperm development was reported to be the walled (= cellular) type. Finally, a greater percentage of seeds germinated from chasmogamous flowers than from cleistogamous ones (47.5 percent vs. 0.07 percent), while ungerminated seeds from both types of flowers usually had endosperm but no embryo, indicating that endosperm may have developed without fertilization.

Species of *Triodanis* are easily propagated, evidently either by seed or vegetatively, and are sometimes grown in flower gardens (Bailey *et al.*).

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Under *Lobelia* see MIRANDA & SHARP. Note that the correct name of *Specularia* is *Legousia* and that *Specularia biflora* = *Triodanis biflora* and *S. perfoliata* = *T. perfoliata*.

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Tribe WAHLENBERGIEAE Endlicher, Gen. Pl. 514. 1838.

3. *Wahlenbergia* Schrader ex Roth, Nov. Pl. Sp. 399. 1821, nom. cons.¹⁰

Erect [ascending, prostrate, or caespitose], terrestrial, perennial [sometimes annual], [rhizomatous] herbs (sometimes woody toward the base) [or shrubs].

¹⁰According to Rickett & Stafleu (Taxon **9**: 122. 1960), *Wahlenbergia* was published by Schrader as a nomen nudum.

Stems several, branched or less frequently simple, often weak and divaricate, pubescent [rarely glabrous], [leaf scars distinct in woody species]. Leaves alternate [rarely opposite], sparser and smaller acropetally, sessile [sometimes subpetiolate or petiolate]; blade elliptic or lanceolate to linear or linear-subulate, glabrous or glabrate adaxially and pubescent to glabrate (with hairs confined to midrib) abaxially, the margin thickened (by hypodermal sclerenchyma visible as a white rim), shallowly dentate to entire [or rarely lobed]. Inflorescences cymose, open, branches alternate and terminated by a single flower or a cymule, bracts narrow; flowers perfect. Calyx actinomorphic; tube hemispheric to oblong-obconical; lobes 5 [rarely 3, 4, or 6], erect, linear. Corolla actinomorphic, funnelform; lobes 5 [rarely 3, 4, or 6], spreading, as long as to twice as long as the calyx lobes. Stamens 5 (rarely 3 or 4), free from the corolla, shorter than the style; filament membranaceous, broadened at the base; anther narrow, caducous. Ovary inferior, semi-inferior [or nearly superior], locules 2–4[–5]; placentation axile; stigma lobes [2 or] 3[–5]. Fruit a turbinate, hemispheric, or elongate cylindrical capsule, dehiscent by 2 or 3 apical pores; seeds amber colored, oblong, lenticular, lustrous. (*Cervicina* Delile, 1813, nom. rejic.) TYPE SPECIES: *W. elongata* (Willd.) Schrader ex Roth, nom. illeg. (*Campanula elongata* Willd., nom. illeg.) = *W. capensis* (L.) A. DC. (*Campanula capensis* L.). (Named for Georg Wahlenberg, 1780–1851, Swedish botanist.)

A genus of 100–220 species, an ambiguity due in part to its uncertain circumscription. *Wahlenbergia* is primarily distributed in the Southern Hemisphere, where it is generally considered to have undergone a development parallel to that of *Campanula* in the Northern Hemisphere. Three groups of species in *Wahlenbergia* were identified by Lothian (1947a) as being geographically and morphologically distinct, but these appear to have remained unnamed, as well as unrecognized, by other workers. The largest of these groups (ca. 90 spp., mostly perennial shrubs), considered to be centered in southern Africa, was thought by Lothian to have evolved from European members of *Campanula* and to have given rise to two smaller groups, one (ca. 20 spp., mostly perennial shrubs) in South America and another (ca. 10 to 12 spp., perennial or annual herbs) in Australasia.

Ecologically, *Wahlenbergia* is extremely variable. The four or five Australian species occupy a wide variety of habitats including xeric ones (Lothian, 1947b), while *W. hederacea* (L.) Reichenb. (Denmark to Spain and Portugal), for example, is a plant of damp, acid, peaty places on moors, heaths, and stream sides (Clapham *et al.*). *Wahlenbergia confusa* Merr. & Perry of New Guinea occurs between 3500 and 4000 m, while other species grow at or near sea level (Tuyn *in* Moeliono & Tuyn).

Wahlenbergia is usually placed in the Campanuloideae. In most systems it is near *Jasione*, and in some of these near *Platycodon* as well. It was, for example, included by A. P. de Candolle with 12 other genera (including *Jasione* and *Platycodon*) in the Wahlenbergieae Endl., a tribe characterized by apical dehiscence of the capsules. Schönland's segregation of *Platycodon* (carpels alternate with the sepals) from *Wahlenbergia* and *Jasione* (carpels opposite the sepals, at least when equal in number to them) is essentially recognized here, except that the subtribe Wahlenbergiinae Schönl., including *Wahlenbergia* and

Jasione, is treated as the tribe *Wahlenbergieae* Endl., which also included *Platycodon* (the *Platycodinae* Schönl. have not, to my knowledge, been recognized at the tribal level; see also family discussion). *Wahlenbergia*, sensu stricto, is evidently most closely related to *Cephalostigma* A. DC. (about seven species in tropical Africa, the East Indies, Brazil, and Peru [Schönland]) and *Lightfootia* L'Hér. (nearly 40 species in southern Africa and one each in Ethiopia and the Mascarene Islands [Schönland]). In fact, there appears to be growing support for the unification of these three genera under *Wahlenbergia*, sensu lato¹¹ (for a review of the problem by supporters of this unification, see Tuyn in Moeliono & Tuyn, Thulin).

Wahlenbergia is distinguished from other campanulaceous genera by a combination of traits, including flowers mostly actinomorphic, stamens free from the corolla, and capsules dehiscing by loculicidal, apical (i.e., within the calyx lobes) valves (vs. lateral dehiscence in *Campanula* and *Triodanis*). Alphonse de Candolle recognized six sections in *Wahlenbergia*, sensu stricto, based on habit, inflorescence characters (including peduncle length), the number of locules per capsule, and seed-surface texture. Three of these sections were further divided, and three were monotypic. Augustin P. de Candolle later elevated sect. *Edraiantha* to the generic level (often *Edraianthus* as a genus); transferred *Codonopsis* A. DC. to *Wahlenbergia* sect. *Megasanthes* (D. Don) A. DC.; combined sect. *Nesophila* A. DC.¹² with sect. *Aikinia* A. DC.; established sect. *Phyteumoides* A. DC.; and retained sects. *Cervicina* A. DC., *Lobelioides* A. DC., and *Linarioides* A. DC. Although the infrageneric classifications of the De Candolles generally have not been accepted in subsequent treatments and revisions (e.g., Von Brehmer, Lothian, Tuyn in Moeliono & Tuyn, Thulin), no formal alternative has been proposed.

Two species of *Wahlenbergia*, each a fairly recent introduction, are credited to the southeastern United States. Section AIKINIA (herbs, often annual, rarely subshrubs; the ovary 2- to 5-locular) of Australasia is represented by *W. marginata* (Thunb.) A. DC. (*W. gracilis* (Forster) A. DC.), $2n = 54, 64, 72$, and ca. 90. (Among recent workers, Carolin is seemingly alone in his opinion that *W. gracilis* is not conspecific with *W. marginata*.) A variable species throughout its wide natural range (China and Japan through southeastern continental Asia and Malaysia to Australia and New Zealand [Tuyn in Moeliono & Tuyn]), *W. marginata* was first collected in North America in Alachua County, Florida, in 1937 (see Ward; see, however, McVaugh, 1945a). Within a few years it was known in Florida from the central panhandle, as well as farther south in the peninsula. *Wahlenbergia marginata* is presently known from stations across the Gulf and Atlantic coastal plains from southern Louisiana to southern North Carolina. It seems to be mostly absent from more interior parts of the Coastal Plain, as well as from southern Florida. However, Shinnars compared its spread

¹¹Although *Lightfootia* is the oldest of the three generic names involved, it is a later homonym of *Lightfootia* Sw. (Flacourtiaceae) and therefore illegitimate. *Cephalostigma* was published in 1830.

¹²In Alphonse de Candolle's *Monographie des Campanulées*, which includes the protolog for this section, *Nesophila* heads the description and treatment of species (p. 160), but *Nesophyla* appears in the *Conspectus Generis* (p. 130).

through the Southeast to that of two other adventives from southeastern Asia, *Digitaria violascens* Link (Gramineae) and *Perilla frutescens* (L.) Britton (Labiatae) and presumed that it would eventually occupy much of the same range (i.e., most of our range, as well as more northern localities in the United States). *Wahlenbergia marginata* grows in sandy or gravelly substrates primarily along roadsides or railways and in sandy pine woods.

The monotypic sect. LINARIOIDES (perennial herbs, with 2-locular ovaries) of South America is represented in the Southeast by *Wahlenbergia linarioides* A. DC. Apparently first collected in North America in 1958 in westernmost Florida (Ward, Godfrey), the species has since been found across the northern portion of the state, but evidently not in the peninsular part. Although the flowers have been reported to be pale blue (vs. purplish blue in *W. marginata*), they are only rarely nonwhite, according to Burkhalter, who has observed the plants for over ten years at numerous places along roadsides and in sandy pine woods in the Pensacola, Florida, area. Compared to *W. marginata*, *W. linarioides* is much less common and widespread in the Southeast, has capsules that open by two (vs. three) apical valves, and has flatter seeds that are otherwise more isodiametric (i.e., nearly circular) (vs. elliptic) in face view. The differences in seed shape are easily discernible in most herbarium material.

Richardson noted a resemblance between plants of *Wahlenbergia linarioides* from Chile and species on the Juan Fernández Islands belonging to sect. NESOPHILA (in part characterized by two-locular capsules), which he considered to be polyphyletic and to demonstrate the convergence often associated with colonization of tropical and subtropical oceanic islands. Such observations are consistent with the notion that existing infrageneric classifications of *Wahlenbergia* seem in general to be unnatural.

The base chromosome number in *Wahlenbergia* is $x = 9$, according to Gadella (1966a), with diploids, tetraploids, hexaploids, and octaploids (i.e., $2n = 18, 36, 54,$ and 72) having been reported (see Bolkhovskikh *et al.*). As indicated above, *W. marginata* demonstrates a high level of infraspecific cytological and morphological variation. The report of $2n = 32$ in two species of *Edraiantha* (see Gadella, 1966b) is consistent with the segregation of this group from *Wahlenbergia* (see A. P. de Candolle), although, for example, $2n = 64$ has been reported for *W. marginata* (Sugiura).

Anatomical features of *Wahlenbergia* include a variously developed leaf hypodermis (as in xerophytic species of South Africa); a clearly defined stem endodermis, sometimes with Casparian thickenings; and medullary bundles in the stem (of some species). The wood of the Campanulaceae has been described largely from observations involving species of *Wahlenbergia* (Metcalf & Chalk, 1950).

The pollen is binucleate when shed in the extraregional *Wahlenbergia bicolor* Lothian (Davis) and trinucleate in *W. marginata* (Subramanyam, 1948). The grains of *W. marginata* are reportedly spheroidal, tetraporate (the pores on slightly elevated parts of the exine), and reticulate, with an outermost layer of microechinate ornamentation (Subramanyam, 1948; see also Dunbar, 1975a, *fig. 12*, for SEMs of other species). Pollen of *W. bicolor* has three pores (Want).

The embryology of *Wahlenbergia* conforms in general to that of the Cam-

panulaceae as a whole (see Subramanyam, 1948), although several features are notable and perhaps unique in the genus. Subramanyam (1948) studied ovule and seed development in *W. marginata* and found that in rare cases it is the third megaspore (instead of the usual fourth) that enlarges, a feature that has also been recorded in *Lobelia trialata* Buch.-Ham. (see Subramanyam, 1948). The synergids are long and show characteristic hooklike projections that have also been observed in *Pentaphragma* (Davis), and although antipodal degeneration is usually in accord with that seen throughout the Campanulaceae, it appears to occur slightly earlier in *Wahlenbergia* (Subramanyam, 1948). Rosén (1932, 1949), who identified in the Campanulaceae three types of endosperm formation (viz. Codonopsis, Phyteuma, Sphenoclea types—see family discussion) that appear to cross taxonomic lines, listed *Wahlenbergia* among genera with the Codonopsis type. Transverse walls are first formed in the chalazal cells in *W. marginata* (Subramanyam, 1948) and *W. bicolor* (Went), but according to Rosén (1949) such divisions usually take place among micropylar cells in the endosperm of Campanulaceae in general. Polyembryony has been reported in *W. gracilis* (Subramanyam, 1947).

Autogamy is the rule in *Wahlenbergia marginata* (Docters van Leeuwen in Moeliono & Tuyn) and may also occur in other species of the genus, even though the stigma opens long after pollen release (Tuyn in Moeliono & Tuyn). Haviland stated that the anthers dehisce introrsely before the opening of the bud, so that the style becomes coated with pollen (glands on the style secrete a glutinous fluid). Cross pollination may be effected when this pollen is subsequently removed by insects (apparently chiefly bees). According to Lothian (1947a), autogamy may also result if the recurving stigmatic lobes encounter pollen when finally contacting the style.

Lothian (1947a) concluded that Australian species of *Wahlenbergia* rarely hybridize in nature, even though this process had been invoked to explain much of the considerable variation observed in the genus. Experimental work by Lothian (1947a) indicated that although several vegetative parts were susceptible to modification by the environment, floral parts were essentially unchanged.

Although propagation is usually by seed, vegetative reproduction by means of stolons, suckers, and pieces of detached root occurs in *Wahlenbergia* (Lothian, 1947a).

According to Muller, Mildenhall's report that in New Zealand *Wahlenbergia* pollen first appeared in the mid-Pliocene is undocumented.

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4. **Jasione** Linnaeus, *Sp. Pl.* **2**: 928. 1753; *Gen. Pl.* ed. 5. 400. 1754.

Erect, ascending, or spreading, terrestrial, biennial (sometimes perennial or annual) herbs. Stems either unbranched or less branched above than near the base, less leafy (or leafless) above than below and often with short, leafy, axillary branches. Leaves alternate, sessile; blade linear-oblong to linear-lanceolate, the apex obtuse or subacute, the margin undulate, entire or remotely and shallowly crenate, ciliate. Inflorescence a terminal globose umbel; flower maturation centripetal; involucre bracts numerous, shorter than the flowers, triangular-acute to ovate-cuspidate, entire, crenate, or serrate; peduncles long, leafless except near the base. Flowers small, numerous, pedicellate, perfect. Calyx actinomorphic; tube ovoid or turbinate; lobes 5, subulate, erect. Corolla actinomorphic; lobes 5, linear, erect to spreading, exceeding the calyx lobes. Stamens 5, free from the corolla; filaments subulate; anthers usually coherent but only at the base (less so to free in bud). Ovary inferior, locules 2; placentation axile; stigma lobes 2. Fruit an ovoid to turbinate capsule, dehiscent by 2 apical pores; seeds amber colored, often much darker at the ends, oblong, lustrous. (Including *Jasionella* Stoianov & Stefanov.) TYPE SPECIES: *J. montana* L. (*Jasione* listed by Linnaeus, *Critica Botanica*, p. 104. 1737 [p. 84 in English transl. by A. Hort, 1938], as a Greek name provided by Theophrastus; name derived from Greek *iásis*, healing.)—SHEEP'S-BIT.

A small, essentially European genus most obviously differing from other southeastern Campanulaceae in its umbellate, involucre inflorescence. Although Linnaeus recognized only *Jasione montana* L. in the first edition of his *Species Plantarum*, nearly a hundred species names have been published since. As it is presently understood, however, the genus includes only 5–15 species, most of which were placed by Kovanda in four informal groups (neither described nor named, although four representative species were indicated). Schmeja (cited in Kovanda), on the other hand, reportedly recognized 13 species in two subgenera.

Jasione has most commonly been allied at the tribal or subtribal level with (among southeastern genera) *Platycodon*, *Wahlenbergia*, and (less frequently) *Campanula* (A. de Candolle, A. P. de Candolle, Bentham & Hooker, Baillon, Schönland). In the system of Fedorov, *Jasione* was placed in the monogeneric *Jasioneae* Fedorov, one of eight tribes comprising the *Campanuloideae*. *Jasione* is included here with *Wahlenbergia* in the tribe *Wahlenbergieae*.

Jasione is represented in the New World and in the Southeast by *J. montana*,

a native of Europe and the Mediterranean region (including parts of northern Africa). Although widely distributed in its native range (to as far as 62° N latitude, and from low elevations more sporadically to the subalpine and alpine zones), the species appears to be most abundant in areas with an oceanic climate. It is best adapted to full sun and well-drained soils (Bailey *et al.*) and is therefore most frequent on sandy soils in pine woods, stabilized dunes, heaths, and dry, grassy places (Kovanda). Of several infraspecific taxa that have been described in this variable species, only two appear to be tenable. *Varietas montana* is a diploid, $2n = 12$, and a strict calcifuge, while var. *littoralis* Fries, $2n = 14$ (an aneuploid), is known only from saline soils in northern Europe; the typical variety is unknown from such habitats (Kovanda; see Tutin regarding var. *littoralis* Boiss., evidently a different taxon).

In North America *Jasione montana* has become established mostly along the east coast from Massachusetts to North Carolina, where it demonstrates the same climatic and ecological affinities prevalent in Old World populations of var. *montana*. Although the species was established and spreading on Long Island by 1925 (Burnham & Latham), it seems to have remained unknown in the Southeast until more recently. It was not included for this region by Small (1933) but was listed about 30 years later by Radford *et al.* as a roadside rarity from Moore Co., North Carolina.

The base chromosome number in *Jasione* appears to be $x = 6$ (Kovanda). Although diploids, tetraploids, hexaploids, and decaploids (i.e., $2n = 12, 24, 36, \text{ and } 60$) have been reported, polyploids are evidently unknown in *J. montana*. Parnell (1982a) found a relatively low recombination index (number of haploid chromosomes plus average number of chiasmata per meiotic cell) and a high percentage of terminal chiasmata in *J. montana*, each considered an alternative to self fertilization (see discussion of breeding biology, below) as a means of bringing about a temporary reduction in the level of genetic recombination.

According to Parnell (1982b), Poddubnaya-Arnoldi showed that the pollen of *Jasione montana* is binucleate. Dunbar (1973b) found it to be similar to that of *Campanula* in shape (spheroidal) and aperture type and number (3 or 4 pores), but different in that the basal divisions of the spinules are less pronounced, the sculptured elements are in a more irregular pattern, the pores lack opercula, and the tectum is perforated. Pollen inviability was shown to vary within inflorescences, among flowers maturing at different times, and within populations of *J. montana*. Plants with very high percentages of inviable pollen (up to 99 percent), as well as completely male-sterile plants, are evidently sporadically distributed throughout the range of the species (Parnell, 1982b).

The ovule of *Jasione montana* in general conforms to that characteristic of the Campanulaceae (see Berger & Erdelska; Erdelska, 1968), except that the integument is so transparent that it is possible to study the living embryo sac (Erdelska, 1968). While the megagametophyte is generally of the Polygonum type, the position of the egg cell is possibly unique among angiosperms in that it usually appears to be separated from the embryo sac wall by the synergids (Berger & Erdelska). Embryogeny appears to be of the Solanad type (see Souèges).

The breeding biology of *Jasione montana* was studied in detail by Parnell

(1982b). Pollen is released onto the hairy, brushlike distal half of the style well before the flower opens. Elongation at the stylar base causes the emergence of this pollen, most of which is removed by insects within a few days. The two stigmatic lobes diverge after about a week, but never reflex enough to come into contact with the style or any of what little pollen might remain on it by this time. Experiments indicated that neither cleistogamy nor agamospermy is an effective means of reproduction in the species (although each may occur), and that the temporal and spatial separation of released pollen and receptive stigma (combined with the early removal of pollen by insects) is very effective in preventing self pollination in nature. Experiments also suggested that, in general, geitonogamy (fertilization between flowers of the same individual) is more effective than autogamy—but less successful than allogamy—under natural conditions. Most insects crawl from one flower to another in each umbel as well as from one umbel to another during a visit to any one plant. Since the flowers encountered are therefore in various stages of development (the outermost in each inflorescence being the most advanced), geitonogamy could be effected.

Jasione montana is the most wide ranging and variable species in the genus. Browsing by animals causes an increase in branching, reduction in umbel size, and change in involucre-bract shape, although genetic and ontogenetic factors also appear to be involved (Pugsley). In addition, there is considerable variation in the degree of pubescence of most above-ground parts, as well as in the color of the corolla. It is unlikely that polyploidy contributes to polymorphism in this species (see above). Environmental modification and genetic recombination are instead the more likely causes (Kovanda).

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Subfam. LOBELIOIDEAE Schönland, Nat. Pflanzenfam. IV. **5**: 63. 1889.

5. **Lobelia** Linnaeus, Sp. Pl. **2**: 929. 1753; Gen. Pl. ed. 5. 401. 1754.

Erect, ascending, or decumbent, terrestrial to aquatic, annual, biennial, or perennial herbs [or shrubs]. Leaves alternate, sessile to short petiolate, variously serrate, crenate, or subentire (often within the same species). Inflorescence a terminal, often loose, bracteate (bracts often leafy) spike, raceme, or panicle. Flowers resupinate [rarely not] at anthesis, perfect [rarely staminate or carpellate, and the plants then dioecious]. Calyx more or less actinomorphic, the tube mostly ribbed and hemispheric; lobes 5, much longer than the tube, entire or often glandular toothed, sometimes with basal appendages. Corolla mostly united below, zygomorphic and bilabiate, the tube usually with an adaxial (after resupination) fissure extending from its apex nearly to its base, through which the stamens and enclosed style and stigma are more or less exerted; the upper (after resupination) lip 2-lobed, the lower 3-lobed. Stamens 5, free from the corolla; filaments connate except at the base; anthers basifixed, connate in a ring around the style, usually the lower 2 shorter and tufted and the upper 3 longer and with incurved tips that partially occlude the anther tube. Ovary half inferior to inferior, 2-locular; placentation axile; style enclosed by the staminal tube; stigma lobes 2, expanding after protrusion beyond anther tube. Fruit a hemispheric capsule with marcescent corolla, stamens, and style/stigma, dehiscent by apical, loculicidal pores [to more berrylike]; seeds yellowish brown, tuberculate, oblong. (Not *Lobelia* Miller, 1754, = *Scaevola* L., 1753, nom. cons.) LECTOTYPE SPECIES: *L. Dortmanna* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **3**: 299. 1913. (*L. cardinalis* L. was selected by M. L. Green in Hitchcock & Green, Prop. Brit. Bot. 184. 1929; a type not designated, according to *Index Nominum Genericorum* **2**: 997. 1979.) (Named for Matthias de l'Obel, 1538–1616, Flemish botanist and herbalist.)

A cosmopolitan genus comprising at least 365 species, according to Wimmer, the most recent monographer of the group on a worldwide basis. A clear majority of the species are native to Australia and Africa, although large numbers are indigenous to Mexico, Central and South America, and various Pacific Islands. Several species occur in China and eastern Asia, but only two are native to western Europe. It is the widest-ranging genus within the Lobelioideae (Wimmer) and is the only one with members in our area. Of the 25–30 species



FIGURE 2. *Lobelia*. a-l, *L. cardinalis*: a, tip of flowering stem, $\times \frac{1}{2}$; b, flower with fenestration (in black) behind nearest calyx lobe at base of corolla, staminal tube with enclosed style and undeveloped stigma exerted through fissure between 2 upper corolla lobes, $\times 2$; c, flower with corolla removed, filaments monadelphous except at base, stigmas just beginning to expand, $\times 2$; d, anther tube formed by connation, the lower 2 anthers shorter and tufted, $\times 4$; e, cross section of anther tube after dehiscence, style in center, $\times 6$; f, tip of style with stylar brush and unexpanded stigmas at time of anther

present in North America, all but a few are confined mostly to the area east of the Mississippi River.

In the Southeast species of *Lobelia* are easily distinguished from other Campanulaceae by characters that separate the two major subfamilies (e.g., they have zygomorphic corollas, connate anthers and upper filaments, and two carpels; see family discussion). The genus was placed by Wimmer in the Lobelioideae (top of ovary conical instead of flat, fruit usually dehiscent instead of indehiscent), one of two tribes recognized in his treatment of the Lobelioideae. *Lobelia* is further distinguished within the tribe by a combination of characters that include a slit between the two adaxial (after resupination) lobes of the corolla, the exertion through this slit of stamens and enclosed style and stigma, and a subglobose to elliptic, pedicellate, bilocular capsule with axile placentation and apical, loculicidal dehiscence.

Lobelia is perhaps most closely allied to *Pratia* Gaudich., of the Southern Hemisphere, even though the latter was placed by Wimmer in the Delisseae Reichenb. (top of ovary flat, fruit indehiscent). Although *Lobelia* and *Pratia* are indistinguishable by floral characters, they were until recently generally accepted as distinct on the basis of fruit type, which in *Pratia* is often a vividly colored berry. Moeliono & Tuyn have reported, however, that although Asiatic and western Malaysian individuals of *Pratia angulata* (Forster f.) Hooker f. (*Lobelia angulata* Hooker f.) produced such fruit, the pericarp in eastern Malaysian material was drier and thinner (almost membranaceous), and the apex became convex and even tardily dehiscent (by two valves). In one case they reported fleshy, indehiscent berries and true capsules in the same collection. Adams indicated that in the West Indies these genera are not separate; Mabberly (1975a) considered them closely allied; and Ydrac showed that they are indistinguishable in vegetative anatomy. Because such observations suggest that the tribes of Lobelioideae proposed by Wimmer are unnatural, they are not recognized here.

The species of *Lobelia* occurring in the southeastern United States were placed by McVaugh (1943) in two of six sections recognized for North American plants (no other infrageneric taxa were designated). Wimmer, on the other hand, placed all of our species in sect. *Hemipogon* Bentham (= sect. LOBELIA), one of two sections comprising subg. *Lagotis* E. Wimmer (= subg. LOBELIA). Section *Hemipogon* was further divided into two subsections. One (or perhaps two) of our species (*L. homophylla* E. Wimmer; *L. Cliffortiana* L. actually may not occur in our area) was placed in subsect. *Leiospermae* E. Wimmer, while the remainder were assigned to subsect. *Trachyspermae* E. Wimmer (= subsect.

dehiscence, $\times 12$; g, expanded stigmas protruding from anther tube, $\times 4$; h, expanded stigmas, $\times 12$; i, diagrammatic cross section of ovary with 2 locules, each nearly filled by an axile placenta and numerous ovules, $\times 6$; j, diagrammatic longitudinal section through half-inferior ovary with numerous ovules and axile placentation, $\times 3$; k, capsule after dehiscence, with persistent calyx, corolla, stamens, and style/stigma, $\times 3$; l, seed, $\times 25$. m, flower of *L. siphilitica*, staminal tube with enclosed style and undeveloped stigma partly exerted through fissure between 2 upper corolla lobes, $\times 2$.

Lobelia). Subsection *Trachyspermae* was divided into two "greges," one of which, grex *Cardinales*, included one of our species (*L. cardinalis* L.), and the other of which, grex *Coelestes* (= grex *Lobelia*), contained the others and was divided into two "subgreges." Subgrex *Dortmanna* (= subgrex *Lobelia*) included the extraregional *L. Dortmanna* L., and subgrex *Kalmia* included the remainder of our species (perhaps 18), forming what could be called a primarily southeastern (United States) assemblage. The relatedness of these approximately 18 species was also recognized by McVaugh (1943), who included them, together with *L. cardinalis*, in sect. *Dortmanna* (= sect. LOBELIA).

From consideration of data including those provided by cytogenetics, Bowden (1959b) recognized four major (but unnamed) lines of evolution among North American species of subsect. *Lobelia* sensu E. Wimmer. In three of these lines, only a single, diploid species remains extant. These are *L. inflata* L. and the extraregional *L. Dortmanna* and *L. Kalmii* L. According to Bowden (1959a), the three do not hybridize either with each other or with any other North American species of *Lobelia*. The fourth major line included three subordinate lines: a group with small (7–15 mm) flowers, one with small to medium (11–33 mm) flowers (and narrow leaves), and a third with medium to large (15–50 mm) flowers.

Primarily for purposes of presentation, I have for the most part followed the infrageneric classification of Wimmer, with Bowden's divisions applied to subgrex *Kalmia* (i.e., all of our species except *L. homophylla*, *L. cardinalis*, and perhaps *L. Cliffortiana*). In general, the species concepts of McVaugh (1943) appear to be sound and are employed here.

Subgenus LOBELIA is characterized by distinctly bilabiate corollas (vs. less distinctly bilabiate or unilabiate corollas in subg. MEZLERIA (Presl) E. Wimmer and subg. TUPA (G. Don) E. Wimmer) that have two more or less erect adaxial lobes. The distribution of the subgenus is largely that of the genus as a whole, with the exception that it does not appear to be as well represented in tropical Africa or on islands in the Pacific Ocean. Section LOBELIA (all of our species) includes plants in which the two shorter, adaxial (lower) anthers are pilose-penicillate apically (vs. all anthers equal in length and pubescence in sect. HOLOPOGON Benth). The pubescence characters of the anthers were not considered by McVaugh (1936) to be of taxonomic value.

Species of subsect. *Leiospermae* have seeds with smooth surfaces. *Lobelia homophylla* is an annual plant with ovate, often crenate (or dentate to serrate) leaves that are cauline but sometimes clustered near the base; basal bracteoles; entire calyx lobes; blue, nonfenestrate corollas; mature capsules that are one-third or less inferior; and ellipsoid seeds. The species occurs in pinelands and along fence-rows and roadsides and is known only from peninsular Florida. *Lobelia Cliffortiana*, $2n = 14$, is very similar to *L. homophylla* but differs in its sometimes lanceolate or elliptic upper leaves, usually larger flowers, and more-than-half-inferior capsules. *Lobelia Cliffortiana* has been reported to occur as a weed in wet places, waste places, and cultivated ground on the Coastal Plain from Florida to Texas (Small, 1933). McVaugh (1940b, 1943) reported that, although it is native to the Greater Antilles, it has been introduced in Trinidad and various tropical and subtropical mainland areas in the New

World, as well as in the Old World tropics. Ward stated that the species has been incorrectly attributed to Florida, evidently through confusion with *L. homophylla*. I have seen no smooth-seeded specimens from the Southeast that do not belong to *L. homophylla*.

Subsection *Lobelia* is characterized by seeds that are markedly roughened. This feature distinguishes all native North American species of *Lobelia* (with the exception of *L. homophylla*) from those of other parts of the world and (according to McVaugh, 1936) indicates a common ancestry for them. Grex *Cardinales* is a North American group of about four species that differ in flower color from grex *Lobelia*, a North American and northern European assemblage (of which only *L. Dortmanna* occurs outside of North America). With the exception of occasional white-flowered plants in both groups, members of grex *Cardinales* have red (vs. blue) corollas. (Such a distinction may be unnatural: some species of grex *Lobelia* [e.g., *L. inflata*, *L. floridana* Chapman] may have pink flowers; and *L. cardinalis* [grex *Cardinales*] may be most closely related to *L. siphilitica* L. [grex *Lobelia*].)

Grex *Cardinales* is represented in the Southeast by *Lobelia cardinalis*, $2n = 14$, a familiar and attractive plant that grows in wet ravines and swamps and along lake shores and streambanks throughout our range. Although McVaugh (1952) considered this species to be most closely related to the northern *L. rotundifolia* Juss. ex A. DC. (but to have evolved somewhere south of central Mexico), Bowden (1959b) hypothesized, in part on the basis of cytogenetic evidence, that *L. cardinalis* is more closely related to *L. siphilitica* and that it evolved in the Southeast. Bowden further proposed that the two commonly recognized subspecies of *L. cardinalis* were derived from ancestral populations in our area. While subsp. *cardinalis* (leaves lanceolate to ovate-lanceolate, blades mostly 3–5 times as long as wide) spread farther north to Minnesota and New Brunswick and west to Texas, subsp. *graminea* (Lam.) McVaugh (leaves linear to ovate-lanceolate, blades mostly 6–12 times as long as wide) migrated along the Gulf of Mexico through Texas and Mexico to as far south as Panama, with a number of varieties evolving in the process. Bowden therefore considered subsp. *graminea* (which does not occur in the Southeast) to have migrated secondarily to the Southwest from Mexico and farther south, whereas McVaugh contended that this migration was a primary one.

Grex *Lobelia* was divided by Wimmer into two subgreges. Subgrex *Lobelia* (leaves linear, bitubulate) is monotypic, including only *L. Dortmanna*, of northern North America and northwestern Europe, while subgrex *Kalmia* (leaves variously shaped, flat), with the exception of *L. Kalmii* L., of northern North America, comprises species that are native to and/or endemic in the Southeast.

Lobelia inflata, $2n = 14, 16$, although small flowered, is somewhat removed from the other small-flowered species in subgrex *Kalmia* (Bowden, 1959a, 1959b). It is superficially reminiscent of *L. Cliffortiana* but has roughened seeds, as well as inflated capsules. It is recognizable in flower by its narrow, entire calyx lobes that often exceed the corolla in length, as well as by the presence of leafy floral bracts in the lower portion of each inflorescence. It differs from *L. spicata* Lam., another small-flowered species with which it is sometimes confused, by its quickly maturing capsules that render the flowering

portion of the inflorescence relatively short. Krochmal and colleagues (1972a) stated that the corollas of *L. inflata* are violet to pinkish white. The species probably originally inhabited dry places in open woods, but has since spread to dry roadsides and waste places. Laboratory work has shown that plants are adversely affected when the soil pH is greater than seven (Krochmal & Magee). *Lobelia inflata* occurs throughout the eastern United States, with fewer localities west of the Mississippi River. In the Southeast it is more common in the northern tier of states and appears to be quite rare on the Coastal Plain.

Lobelia spicata Lam., $2n = 14$, and six other small-flowered southeastern species comprise the first of Bowden's three subordinate lines within his fourth major line in subsect. *Lobelia* sensu E. Wimmer (see above). *Lobelia spicata*, *L. appendiculata* A. DC., and *L. Gattingeri* Gray differ from the other four small-flowered species in their relatively short pedicels that give the inflorescence a spikelike appearance. The three seem to be closely related and intergrade in a number of morphological features, including the pubescence characters by which they are, nevertheless, most easily separated. The calyx lobes are glabrous (or nearly so) in *L. spicata*, glabrous in *L. Gattingeri*, and pubescent in *L. appendiculata*; the bases of the stems in *L. spicata* are for the most part conspicuously pubescent, while those of *L. Gattingeri* are glabrous or sometimes have a few chaffy hairs. *Lobelia spicata* differs from all other small-flowered species in its more congested inflorescences that taper more gradually toward the apex. *Lobelia spicata* occurs throughout most of the area from southeastern Saskatchewan to eastern Texas and New Brunswick; in the Southeast it does not seem to occur on the Coastal Plain southeast of a line from about New Orleans to northeasternmost North Carolina. The plants grow in moist or dry places in woods, fields, and meadows. Several varieties of *L. spicata*, supposedly differing in leaf arrangement, pubescence, and calyx appendages, have been named and are represented in the Southeast but are reportedly connected by intermediates (McVaugh, 1943).

In addition to differences in inflorescences, *Lobelia appendiculata* and *L. Gattingeri*, $2n = 14$, differ from *L. spicata* in their thinner, smoother, sessile cauline leaves that are rounded at the base (vs. tapered to a petiole in *L. spicata*). The two species are closely related and, according to McVaugh (1943), nearly indistinguishable by vegetative characters. Although McVaugh (1936) initially maintained them as distinct species because of the very restricted range of *L. Gattingeri* (see below) and an apparent lack of intermediates, he clearly indicated that such a position was only tentative and later, with no further discussion (1943), treated them as conspecific varieties (*L. appendiculata* var. *appendiculata* and var. *Gattingeri* (Gray) McVaugh). Bowden (1959a, 1959b), however, considered the two entities to be specifically distinct on the basis of a combination of traits including, in *L. Gattingeri*, shorter stems, glabrous (vs. ciliate) calyx lobes, and a lack of auricles, even though McVaugh (1936) had indicated that both the ciliation of the calyx lobes and the length of the auricles were very variable in *L. appendiculata*. It is clear that the situation deserves further attention.

Lobelia appendiculata grows in moist to dry sandy soils in pinelands, open woods, and prairies in central Alabama, Louisiana, and the southwestern half

of Arkansas, as well as in eastern Texas, southern Oklahoma, and eastern Kansas. *Lobelia Gattingeri* is known only from a small area in the limestone region of central Tennessee in seeping or springy places on calcareous bluffs and in cedar barrens (see Baskin & Baskin).

The four remaining small-flowered species generally have longer pedicels and thus more racemelike inflorescences than the foregoing three. *Lobelia Boykinii* Torrey & Gray and *L. Canbyi* Gray, both $2n = 14$, have linear, sessile, cauline leaves and lack the broader basal leaves seen in *L. Feayana* Gray and (often) in *L. Nuttallii* Roemer & Schultes. *Lobelia Boykinii* is a more delicate plant than *L. Canbyi*, with shorter, narrower leaves (not more than 0.5 mm wide). *Lobelia Boykinii* also lacks bracteoles on the pedicel, and it flowers in the spring or early summer; *L. Canbyi* has a pair of bracteoles near the base of the pedicel, and it flowers from July to October. *Lobelia Boykinii*, the only rhizomatous species of *Lobelia* in our area (Godfrey & Wooten), is an often-immersed plant of pineland swamps or cypress ponds (also savannas, see Bowden [1959a] and Radford *et al.*) on the Coastal Plain in northern Florida, Georgia, and the Carolinas, northward to southern Delaware (McVaugh, 1936). *Lobelia Canbyi* usually grows in pineland swamps and savannas in parts of Tennessee, Georgia, and the Carolinas and is evidently confined to pine barrens in Delaware and New Jersey. McVaugh (1936) considered *L. Boykinii* to be a distinct, Coastal Plain species of obscure affinities and (evidently) superficial resemblance to *L. Canbyi*.

Lobelia Nuttallii, $2n = 14, 28$, may closely resemble *L. Canbyi* (plants of each species have linear cauline leaves and a pair of basal bracteoles on the pedicels), especially when the broad basal leaves are absent. (The rosette leaves in this species, and apparently in others including *L. flaccidifolia* and *L. appendiculata*, are sometimes shed prior to anthesis; the persistence of these leaves in *L. spicata* is evidently under a greater degree of genetic control [Godfrey & Wooten].) However, *L. Nuttallii* is a more slender plant (at the base the stem is usually 0.5–1 mm wide, vs. 1.5–3.5 mm), with pedicels that are glabrous or nearly so (vs. densely pubescent) and in length usually greater than or equal to (vs. less than or equal to) the subtending bract. *Lobelia Nuttallii* is frequent among wiregrasses (*Aristida stricta* Michaux) in moist pinelands and savannas, sometimes in brackish marshes or dry places and usually in acid conditions. It occurs from central Tennessee and adjacent Kentucky to Louisiana, Alabama, and northern Florida and northward to Long Island, New York. Brooks & Hauser considered it a probable introduction in southeastern Louisiana.

Lobelia Feayana, $2n = 14$, is smaller and less erect than *L. Nuttallii*, although the two are otherwise quite similar morphologically. The lower stems are usually trailing, uniquely (among our species) rooting at the nodes and sometimes mat forming (Godfrey & Wooten); only the flowering stems are ascending. Although it has rosette leaves similar to those often seen in *L. Nuttallii*, they are often broadly ovate to suborbicular (vs. usually spatulate) and grade (instead of abruptly change) into the cauline leaves, which become narrower toward the apex of the plant (but which are generally neither as narrow nor as numerous as those in *L. Nuttallii*). *Lobelia Feayana* also has more elongate capsules that are two-thirds or more (vs. one-half) inferior. It occurs in moist and/or sandy

places, seashores, swamps, and pinelands, and it is endemic to peninsular Florida (though evidently absent from the southernmost portions of that state, viz., Monroe and Dade counties). *Lobelia Nuttallii* was thought by McVaugh (1936) to have given rise to *L. Feayana* in northern Florida, where the two species now intergrade to some extent.

Four species with mostly narrow leaves and small to medium flowers comprise the second of Bowden's subordinate lines of evolution within his fourth major line in subsect. *Lobelia* sensu E. Wimmer. *Lobelia floridana* and *L. paludosa* Nutt., both hexaploids ($2n = 42$), have large basal leaves and much smaller, less numerous cauline leaves. The species are morphologically close and often indistinguishable by vegetative characters except that *L. floridana* is usually a larger plant. *Lobelia floridana* is most readily distinguished from *L. paludosa* by its almost always nonfenestrate corollas and its longer (at least 3 mm) filament tubes. *Lobelia floridana*, which according to Bowden (1964b) has pink corollas, occurs in moist pinelands and on the borders of ponds in pinelands and cypress swamps. Its distribution overlaps that of *L. paludosa* only in the area of the Apalachicola River in northwestern Florida, and from there it extends along the Gulf Coast to southwestern Louisiana. It is also known from an isolated area in southeastern (coastal) North Carolina. *Lobelia paludosa* is often emergent, growing in low areas in pinelands, as well as in ponds, in southeastern Georgia and all but westernmost Florida.

Two other narrow-leaved species have only cauline leaves, of which the lower ones are usually larger. Both have sessile upper leaves, but the lower leaves are short-petiolate in *Lobelia flaccidifolia* Small (*L. Halei* Small), $2n = 14$, and usually sessile in *L. glandulosa* Walter, $2n = 28$. Compared to *L. glandulosa*, *L. flaccidifolia* has flowers that are more numerous and in tighter, less secund racemes (a difference that persists in fruit). In addition, *L. glandulosa* has fenestrate corollas. Both are Coastal Plain species: *L. flaccidifolia* occurs in river swamps from southeastern Georgia to the northern Gulf Coast of Texas, and *L. glandulosa* grows in swamps and wet places, often in pinelands, from Florida to southern Virginia and perhaps from more isolated localities in Mississippi and Texas.

Six species of *Lobelia* occurring in our area have medium to large flowers and constitute the last of Bowden's three subordinate lines of evolution. *Lobelia amoena* Michaux and *L. elongata* Small, both $2n = 28$, have upright, unbranched, and relatively coarse stems. Bowden (1960a) proposed that each species is of hybrid origin, involving diploid plants that were probably ancestral to *L. puberula* Michaux (see below) as one of the parental species. *Lobelia amoena* differs from *L. elongata* in its elliptic to ovate, rarely lanceolate leaves that are 1.5–4.5 cm broad (vs. narrowly elliptic and usually 1.5 cm or less wide) and its shorter filament tubes (8 mm or less vs. 8–11 mm long). (See McVaugh regarding the identity of these two species and the corresponding type material.) Two varieties, both of which are plants of swamps and moist woods in mountain and piedmont districts, are generally recognized in *Lobelia amoena*. Variety *amoena* has entire (vs. toothed) calyx lobes and shorter filament tubes; it generally occurs in the western parts of the Carolinas, eastern Tennessee, northern Georgia, and eastern Alabama. Variety *glandulifera* Gray (*L. geor-*

giana McVaugh) also occurs in this region but extends onto the Coastal Plain as well, into parts of western Florida and adjacent areas and eastern North Carolina and Virginia. A plant of tidal marshes but also occurring in swamps and on low ground near the coast, *L. elongata* is known from the area between Georgia and Delaware.

Four medium- to large-flowered species are diploids ($2n = 14$). *Lobelia brevifolia* Nutt. ex A. DC. (leaves numerous, short, sessile, divaricate to slightly ascending, short pectinate) and *L. puberula*¹³ (usually with relatively dense stem pubescence) were thought by Bowden (1959b) to have been segregated relatively early in the history of the genus in the southeastern United States. Nevertheless, a close relationship is indicated by the frequency with which they hybridize (Bowden, 1961b; McVaugh, 1936; Ward). Individuals of both species usually have rather weak, unbranched stems, but the calyx auricles of *L. brevifolia* are broad and foliose and usually cover the calyx tube completely, while those of *L. puberula* are generally much smaller. Holroyd stated that the presence of medullary bundles in the stem is probably diagnostic for *L. puberula*, although this feature is apparently rare or unreported for the Lobelioideae in general (Metcalf & Chalk, 1950). Bowden (1960a) discovered a haploid seedling among the progeny of one of his experimental crosses, indicating a low frequency of parthenogenesis in *L. puberula*.

Lobelia puberula occurs in wet places and various kinds of soils in woods, on low ground, and in thickets throughout most of the southeastern United States and adjacent areas. Turner reported it from a "bog" in eastern Texas, intermingled with what he considered the strikingly dissimilar, though closely related, *L. Reverchonii* Turner, a species that enters our range in Louisiana (Rapides Parish). It differs from *L. puberula* in having greater distances between lower flowers (2.5–5 cm), densely hirsute pedicels and calyx bases, recurved lower corolla lobes, and longer corollas (9–15 mm) and anther tubes (4–6 mm). *Lobelia brevifolia* usually grows on damp, sandy soils in pinelands and is restricted to the Coastal Plain from the Florida panhandle to eastern Louisiana, usually near the coast. McVaugh (1936) indicated that on the basis of flower structure this species is related to *L. glandulosa*.

Lobelia siphilitica, $2n = 14$, and *L. cardinalis*, the other two diploid species in Bowden's medium- to large-flowered line, generally produce larger flowers than do any other species of *Lobelia* in the Southeast. Although strong morphological characters separate them, plants of each species are perennials and may be unique among southeastern members of *Lobelia* in that they form offset shoots (see, however, Holroyd, who stated that *L. inflata* and others also demonstrate this type of vegetative reproduction). Bowden considered each to be relatively recently evolved and to have shared a common ancestor with no other extant species. Artificial hybrids between the two are well known (e.g., Ames, 1903; Bowden, 1961a, 1964a, 1964b), but natural hybrids are evidently quite rare, though rather frequently reported (Bowden, 1964a; Ferrenia;

¹³McVaugh (1936) pointed out that the absence of type material makes the exact identity of *L. puberula* and its several morphologic/geographic phases impossible to determine, although later workers (e.g., Bowden, 1960a; Ward) have not reported such a problem.

McVaugh, 1943; Schneck; Steyermark; Witherspoon). Braun reported that they coexisted in the same garden for many years without hybridizing. It seems clear that reproductive isolation between these two species results from the fact that they do not normally share pollinators. Bees usually pollinate flowers of *L. siphilitica*, and although they may obtain nectar from *L. cardinalis* through the fenestrations in the base of the corolla (FIGURE 2b), they need not (and usually do not) contact pollen or stigmas in doing so (Robertson). Pollination in *L. cardinalis* is effected because hummingbirds or long-tongued lepidopterans contact pollen or receptive stigmas while obtaining nectar, which they accomplish by inserting their beaks or tongues into corolla tubes that are too narrow and too long for bees and the tongues of bees, respectively (Trelease). Wood (pers. comm.) observed plants of these species growing side by side at the Montreal Botanic Garden and reported that although some individual honey bees were actively collecting (blue) pollen from *L. siphilitica*, others were getting nectar through the fenestrations in the corollas of *L. cardinalis* without obtaining any of the (yellow) pollen of this species.

Lobelia siphilitica is a wide-ranging species in the United States east of a line from western North Dakota to western Texas, although it is poorly represented on the Coastal Plain in the Southeast. Two varieties are usually recognized. Plants of var. *ludoviciana* A. DC. are smaller and less hairy (to glabrous), with smaller leaves and flowers than those of var. *siphilitica*. They generally occur west of the Mississippi River, usually in wet places on prairies and in the mountains or on limestone cliffs, while individuals of var. *siphilitica* are generally found east of the Mississippi River in moist or wet, neutral to basic soils, often in light shade. Intermediates between the two varieties occur throughout the Mississippi Valley. *Lobelia cardinalis* differs most strikingly from all other species of the genus in our area in its red corollas, and on this basis it was considered by Wimmer to be unrelated to them.

A number of chemical studies have provided systematically relevant information concerning *Lobelia siphilitica* and *L. cardinalis*. Wilson investigated anthocyanin pigments from corollas; he found that a pelargonidin was present in *L. cardinalis*, and a delphinidin in *L. siphilitica* (see also Yoshitama). Gupta & Spenser provided evidence indicating that lobinaline, the major alkaloid in *L. cardinalis*, resulted from the dimerization of a monomer related to 8-phenyllobelol, a simpler alkaloid occurring in *L. inflata*. (*Lobelia inflata* contains all the known "lobelia alkaloids" except lobinaline [Keogh & O'Donovan].) Tschesche and colleagues (1964) suggested that two alkaloids isolated from *L. siphilitica* are chemically related to lobinaline. Bentley and co-workers reported that in *L. cardinalis* the aerial parts are richer in polyacetylenes than the roots, although the opposite is true of a hybrid with *L. siphilitica*; in both species and hybrid the major polyacetylene is enediynetriol.

The "lobelia alkaloids" are well known and are evidently restricted to the laticifers (Mascreé & Crété). At least 14 different pyridine alkaloids have been isolated from *L. inflata* (Kingsbury), although most attention has been directed toward lobeline and related compounds because of their economic value. Flavonoids, triterpenes, and tannins, as well as other types of compounds, have also been detected in two extraregional species of *Lobelia* (Moreira).

Natural interspecific hybrids involving species of *Lobelia* are rare according to Bowden (1961a), with the exception of *L. brevifolia* × *L. puberula*. *Lobelia siphilitica* and *L. cardinalis* hybridize naturally, though rarely (see above), but Braun reported that *L. puberula* readily hybridized with *L. siphilitica* when plants of the two species were grown in the same garden. All five of these species are medium to large flowered, suggesting that such a grouping is indeed taxonomically sound.

Bowden (1961a, 1961b) reported the results of some 1400 attempted crosses involving 21 species of subsect. *Lobelia* (all but two of which occur in the Southeast) and 82 of a possible 420 species pairings. No hybrids involving *L. Dortmanna*, *L. Kalmii*, or *L. inflata* were obtained, supporting the notion that these species represent three distinct lines of evolution within grex *Lobelia*. However, Ames (1901) reported an artificially produced hybrid between *L. inflata* and *L. cardinalis*, and Simonet produced an artificial hybrid between *L. siphilitica* and *L. splendens* Willd. (of Mexico), which was placed in grex *Cardinales* by Wimmer. Such data, together with the affinities suggested above between *L. cardinalis* and other members of grex *Lobelia*, indicate that the segregation of grex *Cardinales* is unnatural.

The results of Bowden's attempted crosses support, to some extent, recognition of his three subordinate lines of evolution, except that this work indicated that the small-flowered group may be somewhat isolated from the other two (as, indeed, Bowden [1954] had earlier indicated). Hybrids were obtained from four pairs of species within the small-flowered group, from one pair within the narrow-leaved (small- to medium-flowered) group, and from nine pairs within the medium- to large-flowered group. Successful crosses were also made between groups, involving one pair of species from the small-flowered and the narrow-leaved groups, two pairs from the small-flowered and the medium- to large-flowered groups, and four pairs from the narrow-leaved and the medium- to large-flowered groups. In all, Bowden obtained hybrids between 21 pairs of species in subsect. *Lobelia*, all within his fourth major line of evolution, in which he put 18 species. In addition to these hybrids, twelve more, each involving the genomes of three to six species, were obtained. With the exception of the narrow-leaved species *L. glandulosa*, which contributed to the formation of six of these hybrids, all of the species involved in these crosses were included in the medium- to large-flowered group.

Several anatomical features in *Lobelia* are worthy of note. An articulated, anastomosing latex system that is mainly confined to leaf and stem phloem probably occurs in most members of the Campanulaceae, but in plants of *Lobelia* it occasionally extends into the pith, and in two extraregional species into all parts of the flower as well (Metcalf & Chalk, 1983). The general absence in the Lobelioideae of sclerenchyma in the pericycle of the stem and around the vascular bundles of the leaf is also notable (Metcalf & Chalk, 1950), as is the presence of medullary bundles in the stems of *L. puberula* (Holroyd). Crystals of calcium oxalate have been reported in *L. inflata*, but Wallis demonstrated that such structures (in leaves) consist only of "fat."

Hewitt reviewed the literature pertaining to ovule and seed development in *Lobelia* and presented a detailed account of these and related topics (including

pollen) based on material of *L. amoena*¹⁴ from the Carolinas. In general features of ovule and seed development, *Lobelia* conforms to the Campanulaceae as a whole, but there are some notable peculiarities. Cooper reported that in *L. cardinalis* the synergids and antipodals function as the chalazal and micropylar haustoria, respectively (*sic*; reversal of order probably inadvertent), instead of the usual condition (in angiosperms) in which the haustoria differentiate from cells of the endosperm (see, however, Subramanyam, 1952). However, Maheshwari determined that the synergids and antipodals in *L. trigona* Roxb. disintegrate at the time of fertilization, and that both kinds of haustoria develop from cells of the endosperm (see also Kausik, 1935; Kausik & Subramanyam, for *L. nicotianifolia* Heyne); Subramanyam (1951) later showed the same condition in *L. cardinalis*. Truly haustorial synergids probably only occur in a few species of Compositae (although detailed and illustrated accounts are lacking), according to Maheshwari, who also reported that the haustoria are formed from the endosperm in *Wahlenbergia gracilis* and *Sphenoclea zeylanica*.

Hewitt's account of ovule and seed development in *Lobelia amoena* is generally consistent with those provided for other species of *Lobelia*, including *L. nicotianifolia* (Kausik, 1938), *L. pyramidalis* Wallich (Subramanyam, 1949), *L. siphilitica* (Crété, 1938a), and *L. trigona* (Kausik, 1935). Polyembryony has been reported in *L. siphilitica* (Crété, 1938b).

Brewbaker reported that the pollen is binucleate when shed in five species of *Lobelia*, including *L. cardinalis*, and indicated that Schnarf's report of a trinucleate condition in the extraregional *L. nicotianifolia* needed to be verified. Nevertheless, trinucleate pollen was indicated for this species by Kausik (1938), for *L. cardinalis* by Cooper, and for the extraregional *L. pyramidalis* by Subramanyam (1949). Hewitt determined that the pollen of *L. amoena* is binucleate, although only fragments (if anything) remain of the tube nucleus at anthesis.

The pollen of *Lobelia cardinalis* is deeply tricolpate and reticulate (Martin & Drew), and essentially the same has been reported for *L. amoena* (Hewitt). The pollen tubes of *L. siphilitica* were found by Halsted (1886) to be variously expanded at the tips in material growing through the style, evidently in contrast to the usual condition in *Lobelia*, and the same was also later observed in *L. cardinalis* among pollen grains germinated in a sugar solution (Halsted, 1887). The tips of pollen tubes of *L. amoena* grown in a sugar solution were not expanded in illustrations provided by Hewitt, suggesting that tip expansion is not artificial and perhaps even indicative of a relationship between *L. cardinalis* and *L. siphilitica*.

Seed germination was studied in several species of *Lobelia* by Muenscher. Light was required by *L. inflata*, *L. siphilitica*, and *L. cardinalis*, but not by several extraregional species. However, although some of the seeds of *L. inflata* germinated after one year, all those obtained from *L. cardinalis* or *L. siphilitica* were dormant. Muenscher suggested that since the seeds of all species were air dried upon harvesting, an additional dormancy was induced in *L. cardinalis*

¹⁴The material studied by Hewitt was all obtained from localities outside the range of *L. amoena* var. *amoena* but within that given for var. *glandulifera* by McVaugh (1943).

and *L. siphilitica*; however, germination tests with fresh, undried seeds were not conducted. In view of the habitat differences between *L. inflata* (dry places) and these two species (wet places subject to periodic drying), a greater drought-induced seed dormancy in *L. cardinalis* and *L. siphilitica* could be seen as adaptive. Barton reported that seed longevity in *L. cardinalis* was increased by drier conditions, lower temperatures, and lower oxygen concentrations.

Baskin & Baskin conducted a detailed ecological investigation of *Lobelia Gattingeri*, an endemic of the limestone cedar glades in the Central Basin of Tennessee. Because its seeds can germinate in either autumn or spring, depending on environmental conditions at the time of seed maturation, the plant may behave as either a winter or a summer annual. Populations were found to be infrequent, as well as small, and to vary greatly in size from year to year, depending largely on seedling survival. Seedling mortality results from low temperatures in the winter and drought conditions in the summer.

Several species of *Lobelia* have horticultural and/or medicinal value; none is known to be a serious pest, although some are poisonous. Appalachian populations of *L. inflata* have provided the principal supply of lobeline, employed in therapy against tobacco use (about 300–400 pounds annually) and as a stimulant, antiasthmatic, and expectorant. Although attempts have been made to bring *L. inflata* into cultivation, it is evident that, compared to this species, *L. cardinalis* yields as much lobeline and *L. puberula* actually yields about 32 percent more (Krochmal *et al.*, 1970, 1972a). Lobeline has also been reported in other species of *Lobelia* (for references see Shah *et al.*).

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